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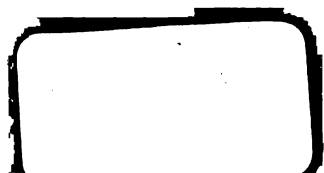
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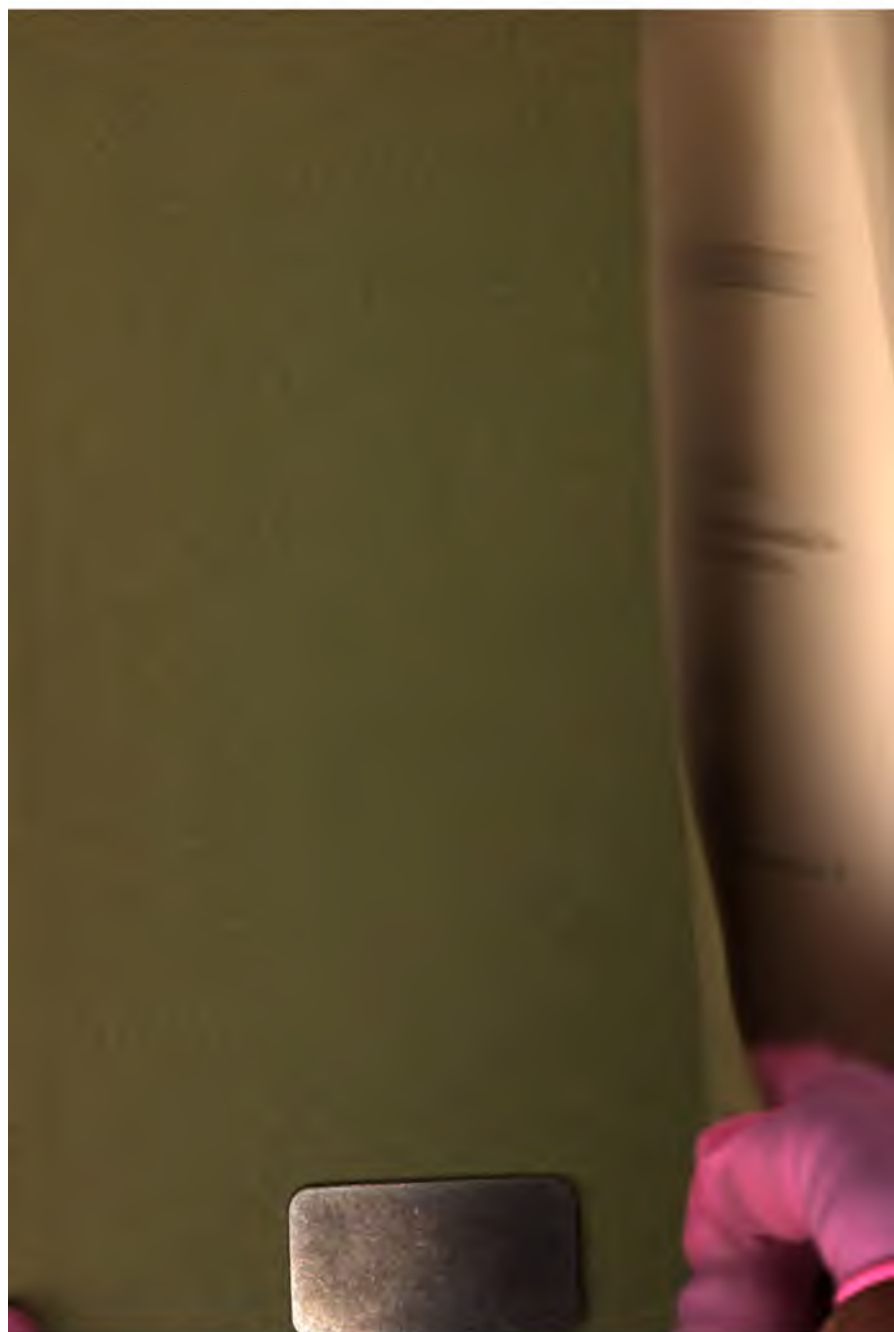
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A
MANUAL OF PHYSIOLOGY.

BY

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SURGEONS, SURGEON TO ST. VINCENT'S HOSPITAL, ETC.**

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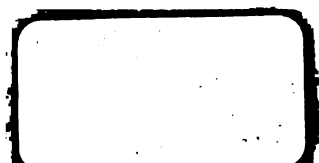
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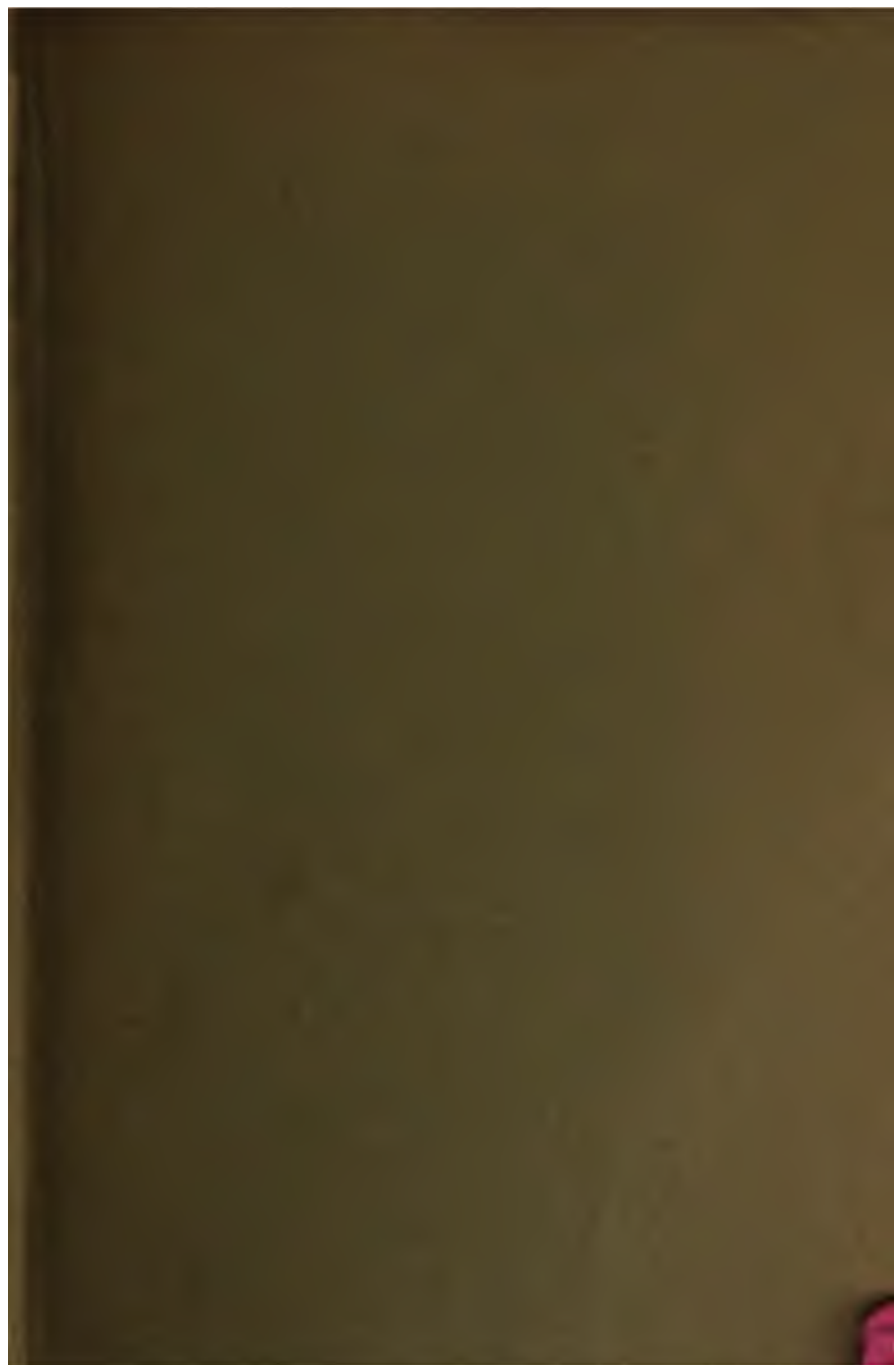
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A MANUAL OF PHYSIOLOGY.



INTRODUCTION.

NATURE OF PHYSIOLOGICAL SCIENCE.

Physiology studies the phenomena of organized beings, and is, therefore, a great department of Natural Science. It is divided into vegetable and animal ; and the latter is subdivided into comparative and human, which last branch of the science is the subject of the present volume, the structure or functions of the lower animals being referred to but incidentally.

There is no branch of knowledge whose limits are more hard to define, nor is there any which requires a more extensive acquaintance with preliminary and collateral sciences, such as Anatomy, Physics, and Chemistry ; and, indeed, the great aim of many recent physiologists is to establish the identity of the laws which govern all vital phenomena with those which preside over the various forms of inorganic matter. On the other hand, so imperceptible is the distinction between most of the normal and abnormal processes, that the physiologist is often compelled to enter the special domain of Pathology ; and this circumstance is the less to be regretted, as no study can be more fitted to introduce the student of Medicine to a scientific comprehension of the principles of disease, or to free its treatment from empiricism.

Foremost among the sciences which aid the study of Physiology proper, is that of Histology. The rapid advances which it has made of late years have thrown a flood of light on innumerable points which, till within a very short time since, were looked upon as entirely mystical in their nature.

New light has also been thrown on many previously obscure points in the functions of the animal body by the study of the various steps in the process of development of the embryo, which, within the last few years, has been carried to such an extent as to elevate Embryology to the rank of a new and distinct science.

Among the vast number of valuable additions which have been made of recent years to our treasury of physiological facts, the great majority have been derived from observations and experiments on the humbler forms of animal life, by means of which sources of information have been arrived at which could never be attained by observation on the human body alone. The general similarity of structure and correspondence of function, enable us to apply the results so obtained to the examination of the laws which govern the vital phenomena of the human organism.

The laws of Physics aid us in the investigation of the laws of motion, both of solids and fluids, and in the determination of the influence of light, sound, heat, and electricity, which are so intimately connected with the functions of the special senses, and the phenomena of muscular action.

A knowledge of the science of Chemistry is indispensable to the physiologist, as an acquaintance with the constituents of the solids and fluids of the human body, and with the variations to which their composition is liable, must be of the greatest possible value in determining the conditions of life.

The Vital Phenomena which the human body manifests have been divided into those which it exercises in common with all other organic beings, and those which are peculiar to animals.

Bichat, the great founder of the science of Histology, maintained that all the peculiar manifestations of animal life were due to certain properties of the tissues, which were diametrically opposed to the physical properties of inorganic matter, and looked upon life itself as one long struggle of the vital forces of the living organism against the external physical forces, which directly tended to destroy it. Magendie vigorously exerted himself to overthrow Bichat's hypothesis of the existence of a vital force, and endeavoured, as far as possible, to reduce the phenomena of the living body to the same physico-chemical laws which govern the various forms of inanimate matter. This idea was worked out by Claude Bernard, with all the untiring energy and enthusiasm which characterized his exertions in the field of this science, to the elucidation of which he devoted his life, and who did not hesitate to affirm, when his ideas on the subject were fully matured, that *all* the manifestations of life were made up of phenomena, identical in their nature with those of the external world.

In examining the physical structure of the body, certain parts may be readily isolated, being obviously subservient to the fulfilment of special offices in the animal economy. These parts are distinguished as *organs*; while the office which has to be performed by each specialized segment of the living organism is known as its *function*. It will, accordingly, be easily understood that the consideration of the functions of the various organs of the living body constitutes the domain of Physiological Science.

CHAPTER I.

SEC. I.—MATTER AND FORCE.

THE great physical law of indestructibility, which has been shown by modern research to apply to both force and matter, must be considered the groundwork on which physical science is based, and demands recognition in considering the phenomena of animated nature, just as in dealing with inorganic substance. The law of the permanence of matter ("*rien ne se crée, rien ne se perd*") was first clearly established by Lavoisier, whilst the principle of the "conservation of energy" owes its existence to the labours of Helmholtz.

Force, or energy, exists in one of two conditions: *actual* (*dynamic, kinetic*) and *potential* (*reserved*). One of these forms of force may be converted into the other; for instance, mechanical movement (*actual force*) may be converted into heat (*potential force*) and *vice versa*. This fact has long been known in a general way, but the exact relation of the two forms of energy was first calculated by Meyer, of Heilbronn (1842), and experimentally demonstrated two years later by Joule, of Manchester. It is now known as the *mechanical equivalent of heat*. The general principle of the relations of the various forms of force to one another is embraced by the term *correlation of forces*, a phrase first employed by Grove.

We have already seen that it is the aim of many of our greatest recent authorities to explain all the phenomena of the living animal organism by the physical laws which preside over the mutations of inorganic matter. But these laws certainly fail, in the present state of our knowledge, to give a satisfactory explanation of a large proportion of the phenomena of life. Accordingly we must still be satisfied to speak of the latter as vital phenomena, without at the same time committing ourselves to the recognition of a distinct *vital force*. The advance

of modern science is gradually encroaching in all directions on the domain of the mystical power of the latter form of energy, and the manifestations of life which remain to be explained by its influence are daily becoming fewer and fewer.

SEC. II.—CHARACTERISTICS OF LIVING ORGANISMS.

THE co-ordination of the phenomena which characterise the existence of animated beings have been explained from time to time by physiologists and philosophers by widely diverging theories. Those which have received most attention are three :—

(1) The *animist* theory (of Stahl)—According to this theory the soul influences the body directly without the intervention of any medium, and regulates all its actions and functions.

(2) The *vitalist* theory (of Lordat)—This involves the hypothesis of an intervening medium between soul and body which regulates, under the direction of the former, all the vital phenomena of the latter.

(3) The *mechanical* theory (of Leibnitz)—According to this theory all the movements and other functions of the living body are governed by the physico-chemical laws which regulate the existence of other forms of matter, and present only the peculiarities of greater complexity and greater difficulty of explanation. The vital organism is a mechanism created and governed by a supreme intelligence and moving under the influence of an original impulse (*pre-established Harmony* of Leibnitz).

A widely diverging form of the mechanical theory is that of the modern evolutionists, according to which the vital manifestations are dependent on external influences, either immediate or remote, and life itself is but a mode of motion which is always provoked, never spontaneous, and the whole science of life forms but a chapter in the science of general dynamics.

Many definitions of life have been given from time to time, but there is none to which exception may not be taken. The following are some examples :—

Aristotle: Life is the sum of the operations of nutrition, growth, and waste.

Lamarck: Life in the parts of a body which possesses it is

the state of things which there permits organic movements, and those movements which constitute active life result from a stimulating cause which excites them.

Bichat : Life is the sum of the functions which resist death.

Richerand : Life is a collection of phenomena which succeed each other during a limited time in an organised body.

Lordat : Life is the temporary alliance of an internal sense and a material aggregate—an alliance cemented by an *ερπυσμον*, or cause of movement, of which the essence is unknown. (This definition applies to man only.)

Beclard : Life is organization in action.

Duges : Life is the special activity of organized bodies.

Treviranus : Life is a constant uniformity of phenomena with diversity of external influence.

P. Berard : Life is the manner of existence of organized beings.

De Blainville : Life is the two-fold internal movement of composition and decomposition, at once general and continuous.

Flourens : Life is a form served by matter.

Ch. Robin : Life is the manifestation of the properties inherent in, and special to, organized substance only. Also : the name of *organization* is given to that state of solution and complex union which semi-solid matters present (sometimes liquid or solid) formed of proximate principles of different orders, and springing from a being, which has had, or has, a separate existence.

Littre : Life is the state of activity of organized substance.

G. H. Lewes : Life is a series of definite and successive changes, both of structure and composition, which take place within an individual without destroying its identity.

Herbert Spencer : Life is the definite combination of heterogeneous changes, both simultaneous and successive, in correspondence with external co-existences and sequences ; or, more briefly : Life is the continuous adjustment of internal relations to external relations.

Küss : Life is all that which cannot be explained by the laws of physics or of chemistry.

Beaunis : Life is the determinate evolution of an organized body, capable of reproducing itself, and of adapting itself to the medium in which it is placed.

It is quite obvious that none of these definitions is of a kind to satisfy the judgment of a critical mind. Each implies, more or less distinctly, the belief in one of the theories above mentioned, or they may all be arranged in three corresponding groups.

Many characteristics seem to distinguish the living body from the various forms of inanimate matter which are found throughout the other kingdoms of nature. Yet in a few these characters are so ill defined as to leave it difficult to decide whether they should be referred to the animal or vegetable domains. We shall consider the leading features of distinction.

PHYSICAL STRUCTURE.—Water is the most important of the compounds which enter into the formation of animal bodies, and in all cases constitutes about two-thirds or three-fourths of their total weight. All the solid parts contain fluids in their interstices. But the more characteristic matters found in the living body are the ternary and quaternary compounds. The latter, especially the albuminoid substances, are distinguished by two striking features: (1) extreme complexity of chemical composition; (2) instability of structure.

Every living body is a heterogeneous mass: if the lowest form of animal life be chosen for examination, or even the smallest possible fragment of any of its tissues, it will be found to be made up of an aggregation of water with colloid and crystalloid materials, but always in certain fixed proportions, and with a definite arrangement. This living mass is the seat of an endless chain of decompositions and recompositions, the vital vortex (*tourbillon vital*) of Cuvier. The complex molecular structure of its constituents cannot be maintained for any considerable length of time, and in order to support the life of the whole, the material for repair must be constantly supplied from the surrounding media to make up for the waste consequent on the incessant metamorphosis of its chemical constituents. A large proportion of the substance of animal bodies is made up of *colloids* (non-crystalline substances, not easily dialysing). It is to their continual whirl that the term "*circulation of matter*" has been applied.

The manner in which the molecules of regeneration are added to the living organism is also distinctive; the new particles always find their way into the interior of the tissue to which they are added, and in this way it contrasts markedly

with the mode of growth of crystalline inanimate matter which takes place by the addition of new particles on the surface. This idea is usually expressed by saying that living bodies grow by *intussusception*, and inanimate structures by *apposition*.

DYNAMIC CHARACTERS.—Living bodies influence physical forces in one of two ways: (1) they set free dynamic energy; (2) they transform one variety of energy into the other. The liberation of dynamic force is exemplified by the development of heat, mechanical movement, &c., and is continuous in the various forms of animal life. In vegetables its effects are less manifest although it is always going on, but its results are very visible at certain periods of their existence (during the time of flowering, germination, &c.)

Transformation of energy is continually occurring in both animal and vegetable organisms: animals chiefly converting potential into dynamic force, whilst vegetables manifest their vital activity by the opposite process. Corresponding to the unceasing exchange between the molecules of dead and those of living matter we have the interchanges between the forces of the external world and those produced within the organism; as the carbonic acid of the atmosphere enters into the formation of the fat of the plant or of the animal, so *solar light, heat, and electricity* reappear in the living body in the form of *muscular movement, of heat, and of innervation*; the vital movements are found to be the correlatives of the physico-chemical movements, as the vital forces are of the physical.

MORPHOLOGICAL CHARACTERS.—Living bodies are *organised*, that is to say, they are formed of parts dissimilar or distinct, arranged in a certain order; this character is found to exist even in the unicellular specimens of animal life, in which we always find a nucleus or, at least, granulations: it is *organic heterogeneity*, which must not be confounded with the chemical heterogeneity already referred to.

The external form of every living being is moulded after a certain morphological type, from which it can deviate only within certain restrained limits during the course of its existence. At the commencement of existence the form is spherical, or nearly so, except in the rudimentary organisms which are made up of a small mass of protoplasm. During the progress of development the typical shape is gradually reached, but even in the mature body the primitive elements of which the

different tissues are made up are found to be minute particles approaching more or less remotely the spherical form of the original cell. *No living structure ever presents the crystalline form*, although crystals may be found enclosed in its interior.

EVOLUTION.—The evolution of every living body passes through certain different phases, which succeed one another regularly, and in a definite order. Every living body has a commencement, an existence, and an end. The crystalline forms of inanimate matter may, in most of these points, be compared to an animated body, but they are distinguished from the latter by the absence of the continual waste and repair—by the fixity of their molecules during the whole period of their evolution. But even this qualification must be made with some reserve; for we know that when a broken crystal is placed in the mother liquid it undergoes a process of repair.

The higher grades of living beings all present a certain individuality. In certain of the lower classes of animals and plants, however, this peculiarity entirely disappears, to be replaced by an intimate solidarity.

Every living organism springs from a *germ*. This was developed by a pre-existing parent endowed with life, and the mature individual in its turn possesses the power of reproducing a being more or less similar to itself, or, to express the idea in a more generalised form, there is always at some period of its life the possibility of one or more detached parts of the body leading an independent existence.

Living beings, accordingly, form a continuous series or chain, which can be traced backwards, link by link, to the date of the first appearance of life on the surface of the earth. Another direct sequence of the general law of reproduction is that the offspring possess characteristics more or less closely resembling those of their parents. The distinctive peculiarities are transmitted—sometimes directly, sometimes in interrupted series. The law of transmission in the former mode is known as *heredity*, in the latter as *atavism*.

The chemical composition of the living body varies with age, and this variation affects both the quantity and the quality of its constituents. The most remarkable and important of these changes is the gradual diminution of the amount of water in the organism as age advances. It is chiefly to this

that the loss of elasticity is due, and indeed from the retrograde nature of the changes which occur with advancing years, such as the development of woody fibre in plants, with its increasing density, the calcification of cartilage, &c., that occurs in the human body in old age, it would appear that living organisms, as they approach the termination of their evolution, gradually approach, in chemical composition, the nature of inorganic matter.

The production of energy also undergoes some modifications during the life of an organism. It usually decreases after having reached its *apogée* (*maximum vital activity*). This rule does not, however, always hold good, as certain living beings present alternate phases of repose and of movement, as seen in hibernating animals, in the metamorphosis of insects, &c. In other organisms the vital functions appear to be completely suspended for an indefinite time, as in the cereal grains, in *rotiferæ* when dried, &c.

The form of living organisms is not less variable; from the spherical shape of the initial period of its existence it undergoes a gradual modification till it reaches the morphological type which characterises the species to which it belongs. This change of shape is accompanied by two correlative phenomena: an augmentation of the bulk of the mass, and the development of its organization. The causes of the arrest of growth are extremely obscure, but are probably due to some change in the proportions between the amount of waste and that of repair.

Death at last comes to terminate the period of vital evolution, and deliver the organism to the action of the external media, which in time reduce it to the elements of which it was originally composed. In complex organisms, at least, death of the body as a whole (*somatic death*) precedes that of its constituent parts (*molecular death*).

ACTION OF MEDIA.—The surrounding media furnish the materials necessary for the maintenance of the individuality of the living body; they furnish the movements which are indispensable for the manifestations of vital phenomena, light, heat, &c.; it also modifies the form of organisms, as we see in the influence of weight, darkness, &c., on vegetable growth, and even in the artificial distortion of the human frame which pernicious customs make fashionable among some races.

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The medium acts upon the living organism at each moment of its evolution ; and its action is of two kinds, regenerative and destructive. All living beings are endowed with *variability* within certain limits, and this variability is an indispensable condition of their existence. Each external action is followed by an internal reaction of the organism which exactly corresponds to the former, and life is, in fact, but an uninterrupted series of adaptations of internal reactions to external agencies.

To recapitulate, the essential characters of life are the following:—

(1). Molecular complexity, heterogeneity, and chemical instability of the organic compounds.

(2). Incessant waste and repair of organic material.

(3). Development of dynamic energy, particularly in the form of mechanical movement, of heat and of electricity.

(4). Organisation.

(5). Definite course of evolution from origin to death.

(6). Origin from a pre-existing individual, and power of reproduction.

(7). Variability and power of adaptation to media, and to external forces.

SECTION III.

DISTINCTIVE CHARACTERISTICS OF ANIMAL AND VEGETABLE LIFE.

Life is manifested in the form of one of two great varieties, the animal and the vegetable. The line of demarcation between these two forms is by no means so sharply defined as is popularly believed, and when we come to examine the lowest specimens of the series, we meet with some individuals the vital phenomena of which cannot be said to be characteristic of either kingdom. This has led many naturalists of high authority to group such organisms in a separate kingdom, not intermediate, but inferior to both, a kind of common stock from which, by bifurcation, sprang the two branches (*protozoa*, *protista* of Hæckel). But having made this reserve, we may say that the characteristic differences between the vegetable and animal kingdoms are very well pronounced indeed.

A plant possesses the same essential chemical elements as an animal—oxygen, hydrogen, nitrogen, carbon, but is distinguished

by the great predominance of the carbon, and its comparative poverty in nitrogenous compounds. Of the mineral salts, alkaline carbonates are found to predominate in plants, and phosphates in animals. The most important of the chemical characteristics of plants is the presence of the colouring matter, *chlorophyll*, which plays an essential part in the life of the vegetable, nevertheless its presence is not an essential character, for it is absent in one class of plants, the fungi, while it is found in certain animals, such as the *hydra viridis*, *euglena viridis*, *stentor polymorphus*, &c. The chemical transformations are less rapid in the vegetable than in the animal, and the chemical stability of the former is greater, still the processes of assimilation and of dis-assimilation are always going on, and a continual process of absorption of oxygen and elimination of carbonic acid gas exists, constituting a true vegetable respiration, identical in its nature with the more obvious form which prevails throughout the animal kingdom. The process of assimilation in the plant is much more complex than that in the animal; it absorbs (from the air and earth) water, carbonic acid, and ammonia; and, from these comparatively simple substances it forms the starch, fatty matter, and albuminoids of the tissues. The animal, on the other hand, has but to utilise these materials when already formed by the plant, while it eliminates the products of dis-assimilation chiefly in the form of water, carbonic acid, and ammonia. So that the principles which are necessary to the life of a plant are precisely those which are eliminated by the animal as the last stage of metamorphosis, and accordingly between earth and air, animal and plant, a correlation and intimate bond of union are found, which are kept up by this series of incessant changes, constructing a veritable *material circulation* (*circulation materielle*, Beaunis).

The development of dynamic energy is very small in the vegetable as compared with the animal organism, and is reserved for certain phases of its existence (germination and flowering), and in special individuals (sensitive plant, &c.) The transformation of energy is the reverse of what occurs in the animal kingdom: a plant changes dynamic energy (heat and solar light) into potential, while an animal transforms potential into dynamic.

The vegetable organisation is less complex; the division of physiological labour is not carried out to such an extent as in the animal kingdom, but it is a difference in degree, not in kind,

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and in the very inferior animals it hardly surpasses that of the vegetable economy.

The leading distinctive characteristics of plants and animals may be briefly tabulated as follows:—

<i>Plant.</i>	<i>Animal.</i>
Presence of chlorophyll.	Absence of chlorophyll.
Predominance of assimilation over dis-assimilation.	Predominance of dis-assimilation over assimilation.
Absorption of water, carbonic acid, and ammonia.	Absorption of oxygen.
Elimination of oxygen.	Elimination of water, carbonic acid, and ammonia (urea).
Feeble liberation of dynamic energy (movement and heat).	Active liberation of dynamic energy (movement, heat, innervation).
Transformation of dynamic into potential energy.	Transformation of potential into dynamic energy.
Voluntary locomotion not present.	Voluntary locomotion.
Sensibility not present.	Sensibility.
Organisation less complex.	Organisation more complex.
Tendency to polyzoism.	Tendency to individualisation.
Growth nearly indefinite.	Growth arrested at a given time.
Variability greater.	Variability less.

But we must remember that none of these characters is absolute: not the absence of chlorophyll, nor movement, nor sensibility, nor digestion, nor respiration; not one of these furnishes a true criterion of animal life. The more exact researches of recent days all tend to break down the barrier which was formerly supposed to separate the two great divisions of animated nature, and unexpected facts are continually cropping up which multiply the points of contact between the animal and vegetable kingdoms. Trees have been found—the *pelo de vaca* of Venezuela, and the *masaranduba* of Brazil—which furnish a liquid whose physical properties and chemical composition closely resemble those of milk. The so-called carnivorous plants, especially the *droseracea*, have been shown by Darwin, and others, to secrete a liquid which is able to digest insects and animal matters when placed in contact with their leaves, while Group-Besanez has demonstrated in malt, in the grains of the *vicia sativa*, of *cannabis sativa*, of *linum usitatissimum*, and in the juice of the urns of the *nepentha*, the presence of a ferment which appears to be identical with pepsin, and possesses the power of digesting albuminoids.

CHAPTER II.

SEC. I.—MAN'S PLACE IN THE ANIMAL KINGDOM.

IF we examine the various forms of animal life from the simplest to the most complex, we shall easily observe that the organization becomes elaborated by almost imperceptible degrees as we ascend the scale. Beginning at the lowest point, we find unicellular organisms, each formed by a microscopic mass of protoplasm, apparently homogeneous in structure (*monera* of Hæckel); the first step in developmental advancement is found in the differentiation of the superficial layer of the protoplasmic mass into a denser membrane or cell-wall; then organs of locomotion appear, either temporary, as in the *pseudopodia* of the *radiolaria*, or permanent, as in the vibratile cilia of some infusoria; organs of reproduction are next developed, as in the nucleus and nucleolus of the infusoria. This scale of gradual development is traceable step by step till we arrive at the highest degree of functional specialization as met with in man. The progressive specialization of organs and of functions can be followed not only throughout the animal series, but even in the evolution of a single organism. If, for instance, we take man from his origin, we find him at first represented by a single cell, the ovum; he represents in this phase a unicellular animal. This cell then segments, and the division repeats itself till a mass of cells are formed, all identical in size and shape, and the segmented ovum now resembles a rhizopod deprived of its pseudopodia. Soon a part of these cells are set apart from the others to form a denser layer, and this again forms three leaflets from which all the organs are found to be derived, and each of the stages through which man passes during the period of embryonic development corresponds pretty closely to the mature condition of one of the inferior members of the animal kingdom.

The analogy is still more striking if, instead of comparing the different stages of the development of man to animals already fully formed, we compare them to different stages of the development of other animals; the resemblance will then be found very close indeed.

Anatomically and physiologically man belongs to the order *primates*. This order includes five families :—

- (1) *Man*;
- (2) *Anthropoid Apes*; including five genera : gorilla, chimpanzee, tschego, orang, Gibbon.
- (3) *Catarrhines*, or monkeys of the old world ; of which the genera are : *semnopithecus*, *colobus*, *cercopithecus*, *macaque*, *magot*, *cynocephalus*.
- (4) *Platyrrhines*, or monkeys of the new world ; genera : *alonate*, *ateles*, *lagothrix*, *cebus*, *pithecia*, *brachyurus*, *callithrix*, *saimiri*, *nyctipithecus*, *arctopithecus*.
- (5) *Lemurs*; genera : *indris*, *propithecus*, *makis*, *hapalemur*, *cheirogaleus*, *loris*, *potto*, *microcebus*, *galago*, *tarsius*, *cheiromys*.

Common Characters.—The same plan of organization is found in man and the anthropoid apes, not only in the more striking outlines, but even in the minute details. Accordingly, we shall limit our enumeration of common characters to those which are found to fail in the inferior monkeys.

The vertebral column of the gorilla and of the chimpanzee possesses the same number of vertebræ as that of man. It is true that the gorilla seems to have thirteen dorsal vertebræ, but what really exists is that the transverse process of the first lumbar vertebra is detached, forming a thirteenth rib. The pelvis has the same general form as that of man, only differing in being narrower and more elongated. In the other apes its form approaches that of quadrupeds. The torsion of the humerus is, as in man, at an angle of 180° , and the olecranon is flattened from before backwards. It is flattened transversely in other mammals. The skeleton of the hands and feet correspond, and, as conclusively proved by Huxley, the name of *quadrumana*, given long ago by Tyson, and adopted by Buffon and Cuvier, should be rejected, as these animals are really bipeds and bimana.

The brain of man and of the anthropoids possesses four distinctive characters which are absent in other animals :—

- (1) A rudimentary olfactory lobe ;
- (2) The posterior lobe of the cerebrum completely covering the cerebellum ;

- (3) A well marked sylvian fissure ;
- (4) A posterior cornu of the lateral ventricle.

The muscular system, with slight exceptions to be mentioned afterwards, presents the same arrangement in man and anthropoids, and it is a remarkable fact that one muscle, the *acromio-basilaris*, which is present in most of the anthropoid apes, is absent in the gorilla as well as in man. The glutæal callosities are absent in anthropoids ; the nails have the form of those of man ; the organs of sense present the same structure.

The vermiform appendix, which is absent in other apes, is present in anthropoids ; the liver is similar in form to that of man, also the lungs and the azygos single lobe, which is present in the inferior apes, is absent in anthropoids as in man.

The posture is biped ; and the attitude of the body, slightly oblique, approaches the vertical more nearly than the horizontal. In the lower monkeys the attitude is decidedly horizontal. During progression they make but slight use of the anterior limbs ; they never rest on the palm of the hand, but on the dorsal surface of the fingers slightly flexed. The palmar surface of the hand never becomes plantar (Broca). The movements of the superior limbs are analogous to those of the arms of man, and the excursion in supination, which in the lower monkeys amounts but to a right angle, in anthropoids attains a range of 180° (Goodsir).

The resemblance of the anthropoids to the human being is very close in early life, but diminishes with advancing years. At birth the resemblance of the foetus is very striking, and in the early years of life they are proportionally more intelligent, as well as being more docile and affectionate. But with advancing years bestial characteristics, physical as well as psychological, gradually develop, and always predominate in the adult.

Distinctive Characters.—The cranial capacity is much greater in man than in the anthropoid apes, the lowest figure met with in case of the human skull was one by Morton of 970 cc. ; while the highest recorded of the gorilla is 539 cc. Human crania have been found whose capacity amounted to 1781 cc., so that the range of difference between human skulls is much greater than that between those of man and the gorilla.

The foramen magnum in the gorilla is placed in the posterior third of the base of the skull ; the facial bones, especially the maxillæ, predominate over those of the cranium proper ; the

superciliary arches are thick, prominent, and overhang the supra-orbital. In man the occipital condyles are within the median fifth of the base of the skull, and the foramen magnum looks downwards and either a little forwards or but very slightly backwards. The sagittal and lambdoid crests are absent, and the orbits and jaws are relatively smaller. The distance between the zygomata is either less than the greatest transverse diameter of the calvaria or exceeds it but little. The prominence of the mastoid processes, of the mental eminence, of the genial tubercles, and of the anterior nasal spine are distinctive of man's skull. The last mentioned prominence has been said by Alix to be an unvarying distinction of man's skull, but, as pointed out by Hamy and Broca, it is often absent in the negro.

The direction of the plane of the foramen magnum is intimately related to the posture of the animal. Three angles have been described in connection with it:—(1) The *occipital angle* of Daubenton, the apex of which is at the central point of posterior lip of foramen magnum (*opisthion*), and the sides formed by two lines, of which the lower is drawn directly forwards in the median occipital plane, and the other from the opisthion to the median point of the inferior margin of the orbit (*point sous-orbitaire* of Broca). (2) The *occipital angle* of Broca, of which the apex and inferior boundary are the same as those of the last, while it is limited above by a line from the opisthion to the *nasion* (point of intersection of the internasal and nasofrontal sutures). (3) The *basilar angle* of Broca, of which the summit is at the *basion* (central point of anterior lip of foramen magnum), the lower side in the occipital plane, and the upper formed by the line between the basion and the nasion.

The following table shows the relative magnitude of these angles in man and the anthropoid apes:—

	Occip. angle of Daubenton.	Occip. of Broca.	Basilar of Broca.
Man ..	.. $-1^{\circ}.5$ to $+9^{\circ}.3$	$10^{\circ}.3$ to $20^{\circ}.1$	$14^{\circ}.3$ to $26^{\circ}.3$
Chimpanzee ..	.. 26.2	35.5	45.5
Orang ..	.. 31.2	45.2	55.2
Gorilla ..	.. 32.5	44.6	53.2
Gibbon ..	.. 31.5	40.6	51.5
Pithecius ..	.. 19.6 to 23.8	33.3 to 35.3	45.6 to $49.$

This table shows us that the angles given vary directly with the posture of the animal in progression; in quadrupeds the

angle which the plane of the occipital foramen forms with the horizontal may be as much as a right angle.

With the view of forming a rough estimate in the living body of the relative intracranial capacity of man and animals, various external measurements have been proposed, the more important being certain angles which are bounded by lines whose directions can be ascertained with moderate ease on the living head. Those easiest of application are the facial angles, of which four have been proposed :—

(1). The first was suggested by Camper (1786). His facial angle is enclosed by two lines called respectively the *horizontal* and the *facial*. The former was drawn from the lower border of the opening of the meatus auditorius externus to the lower border of the opening of the anterior nares. The facial line forms a tangent to the two most prominent points of the face—the glabella above, and the anterior surface of the upper incisor teeth below. The apex is therefore at the point of intersection of these lines, which may be in front of the anterior surface of the superior maxilla, as in the negro, or behind this surface, as in most of the lower animals, or at the anterior nasal spine as in the Caucasian race.

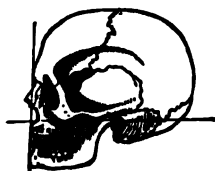


Fig. 1.—Camper's Facial Angle (85°).

(2). The second angle was proposed by Geoffrey St. Hilaire and Cuvier (1795). The facial line of Camper was retained, but the horizontal line was replaced by an oblique (or *auriculo-dental*) line reaching from the same point behind to the free border of the upper incisors below, where, of course, the apex of the angle was then placed. It was soon abandoned, on account of the difficulty of defining its boundaries in many animals.

(3). The third angle is that of Cloquet (1821). Its apex is at the central point of the free border of the superior alveolar arch (*point alvéolaire* of Broca), and from this point two tangential lines are drawn, one to the glabella, and another to the lower border of the external auditory meatus.

(4). The fourth is that of Jacquart (1856). Its apex is at the anterior nasal spine, from which two tangents are drawn, as in the one last described, a facial to the glabella, and a horizontal to the lower border of external auditory meatus.

The angle of Jacquart varies with five conditions:—(1) The prominence of the nasal spine, which, as Broca has pointed out, is very prominent in the white races and almost nil in the negroes; (2) the prominence of the glabella; (3) the elevation of the external auditory meatus above the base of the skull; (4) the amount of elongation of the face (*prognathism*); (5) the development of the anterior part of the brain. Camper's angle varies with the same causes excepting the first, which does not influence it, and the angle of Geoffrey St. Hilaire and Cuvier is similarly changeable.

The facial angle of Camper, which is the one most generally known, varies from 70° to 80° in man, while in the anthropoid apes it ranges between 30° and 40° . This however does not hold good in the very early life of the latter, when it may be as much as 60° . In the chrysothrix it even reaches 66° .

The magnitude of the *cranio-facial angle* has been suggested by Huxley as an index of cerebral development. It is enclosed between the *basi-cranial* and the *cranio-facial axes*, of which the former is formed by a line leading from the basion to the sphenothmoidal suture in the median plane of the skull, while the latter is the line between the alveolar point and the anterior extremity of the other. The greater this angle the greater will the development of the facial bones be found in proportion to those of the cranium proper. In man it varies from less than 90° to 120° . In the anthropoid apes it is very much greater.

The *sphenoidal angle* is one which has been suggested by Welcker as an index of similar import. The lines including this angle are drawn from the anterior margin of sella turcica in median plane of skull, one to the nasion, the other to the basion. Like the other it decreases with the increase of cerebral development.

Absence of the premaxillary bone was formerly believed to be characteristic of the human skull, but, as was shown by Vicq d'Azyr and Goethe, and more fully demonstrated by later observers, this bone is always present in man, but on account of its very early union with the superior maxilla it had remained unnoticed. The premaxillo-maxillary suture is not discernable on the face after birth, but often may be noticed on the palate.

The articulation of the great wing of the sphenoid with the parietal bone is also distinctive of the human skull (Owen). In the anthropoid apes a bridge, formed by the meeting of the

frontal and temporal bones, is interposed between the other two, but this is not unfrequently seen in the human skull, especially in the inferior races. To the first of these forms of suture Broca has applied the term *pterion en H*; to the second the *pterion retourné*. When the frontal and temporal bones meet at a single point, a *pterion en K* is formed.

The order of closure of the cranial sutures presents some differences; the sutures at the base of the human skull are closed before those of the vault, and especially before the frontal suture; the contrary is the case in the anthropoid apes. The early closure of the frontal suture in the latter arrests the development of the brain, while the prolonged patency of the sutures of base of skull accounts for the predominance of facial development.

In anthropoids the canines spring high above the level of the surrounding teeth, and each is lodged when the mouth is shut in an interval (*diastema*) in the opposite dental arch. The date of eruption also differs; in man the canines appear before the second and third molars; in the gorilla they appear after these teeth; but this rule is not constant.

The cerebral convolutions are less developed than in the human brain, and the cortical layer of grey matter is much thinner. According to Bischoff the arrangement of the cerebral convolutions is not the same in man as in anthropoids; and, to trace the analogy, foetal brains of both species should be examined. He also points out that the process of the anterior lobe of the cerebrum, which occupies the olfactory fossa, is present in anthropoids, but absent in the brain of man. Gratiolet has shown that the order of development in the brain of anthropoids is the reverse of what obtains in the brain of man; in the latter the anterior convolutions are the first to appear, in the apes they are the last. He was, however, able to detect only one morphological character which (as he thought) completely differentiated the brain of man from those of all anthropoids. Connecting the occipital lobe behind with the parietal and temporal in front are four convolutions, *plis de passage* of Gratiolet, the *annectant convolutions* of Turner and Huxley. The first and second of these are the distinctive ones. In man they are always large and prominent on the surface, so as almost entirely to mask the perpendicular sulcus. In the orang, the internal or first of these alone is superficial, the second is

hidden at the bottom of the perpendicular sulcus. In the chimpanzee, the internal is entirely absent, and the external is hidden at the bottom of the fissure, so that the latter becomes most prominent. The type of the orang is found in the gibbons and the *sempiterni*, and that of the chimpanzee is repeated in the macaques and the *cynocephali*. In the *guenons* a fourth type is observed; both of the characteristic convolutions are present, but are hidden at the bottom of the perpendicular fissure so as not to appear on the surface. But the presence of both these convolutions has been demonstrated by Broca in *ateles* and *cebus*, so that it has ceased to be distinctive of man's brain.

The hand resembles the human hand, excepting that the thumb is a little smaller, especially in the orang, in which it often wants a nail; the carpus of the orang has an *os centrale*, but the carpus of the gorilla is analogous to that of man.

A similar resemblance exists in case of the lower limb, excepting that the articulation of the great toe is much looser, and that the first metatarsal bone articulates with the internal surface of the internal cuneiform: this arrangement permits a certain amount of abduction, but not a true opposition of the great toe.

In the muscular system there are a few points to be noticed. A tendinous slip descends from the tendon of the *latissimus dorsi* to the *epitrochlea*. In the orang the three parts of the *pectoralis major* are separate. In the chimpanzee the *pronator radii teres* has usually no coronoid origin, nor has the *flexor digitorum sublimis* a radial attachment. The gorilla has a small *trachelo-acromial* muscle. The gibbon possesses a *glutæus quartus*; the *pyriformis* is united to the *glutæus medius* in the chimpanzee and gorilla. In the orang the *pollex* and *hallux* have no long flexor tendons, and the *flexor hallucis* arises from the outer condyle of the femur. The chimpanzee and orang have an ill-developed *flexor accessorius*, and the *transversalis pedis* is absent in the latter. The former has a double *tibialis anticus*, and the *flexor longus hallucis* supplies the first, third, and fourth toes, while the *flexor digitorum* supplies the second and fifth as it does in the orang. The only muscles which exist in man, but have not yet been found in any ape, are the *extensor ossis metacarpi pollicis* and the *peronæus tertius*.

The orang, chimpanzee, and gorilla possess laryngeal sacs, but they are only developed after birth, and apparently by the

influence of vocal efforts. In man they are represented, though on a greatly reduced scale, by the ventricles of Morgagni.

The genital organs present some characteristics. The os penis is present in all anthropoids, and the glans penis is cylindrical. That of the orang approaches the human type most closely, as it has a small prepuce and a fraenum. The clitoris is more voluminous than in the human species. In one variety, the loris, the clitoris is nearly as large as the penis of the male, and similarly perforated by the urethra.

The proportions of the upper and lower limbs are different. The following table from Huxley gives the relative lengths :—

	European.	Bosjesman.	Gorilla.	Chimpanzee.	Orang.
Vertebral Column,	100	100	100	100	100
Arm ...	18	78	115	96	122
Leg ...	117	110	96	90	89
Hand ...	26	26	36	43	48
Foot ...	35	32	41	39	52

From the greater proportionate length of the lower extremity in man, the hands reach but to the middle of the thighs ; in the orang they reach to the ankles. The long neck of the femur is a prominent feature in the human skeleton. The pelvis of man is also more expanded laterally, the transverse diameter between the iliac crests is greater than the depth of the cavity. Other peculiarities of the human body are : pollex long and strong, reaching to middle of basal phalanx of index digit. Tarsus half the length of foot, and the superior articular surface of the astragalus looking almost directly upwards and hardly at all inwards. Hair scanty and very short, except on crown of head, axillae, pubic region, and on front of thorax. On the skin of the palmar surface of the hand two well-marked folds are present ; the anterior is produced by movements of flexion, the posterior by the opposing movements of the thumb. The latter is characteristic of the human hand (Alix), but may occur in the chimpanzee (Broca).

From what has been said we can clearly see that, either anatomically, or physiologically, there is no well-defined line of demarcation between man and the individuals immediately below him in the animal scale, and that it is to his psychological attributes that we are to look for the distinctive characteristics which separate him from all other animals, even those most nearly allied in physical conformation. His mental powers and

susceptibilities, his lofty aspirations, the possession of a moral sense and a religious belief, and the peculiar endowment of articulate language are the distinctive attributes of *homo sapiens*. His varied powers enable him to render all nature subservient to his purposes; the arts of writing and printing have placed at his disposal the accumulated wisdom and experience of former generations as well as of that of the present day, while his omnivorous appetite and capability of adaptation to all climates and all regions, by modification of clothing, &c., combine to constitute man the veritable lord of the creation, and to separate him by a gulf of immeasurable depth from those animals which bear to him the closest structural resemblance.

SEC. II.—VARIETIES OF THE HUMAN RACE.

The various races of mankind have been classified according to affinity of language, local distribution, and, what is more in our way in the present work, according to their structural and functional peculiarities.

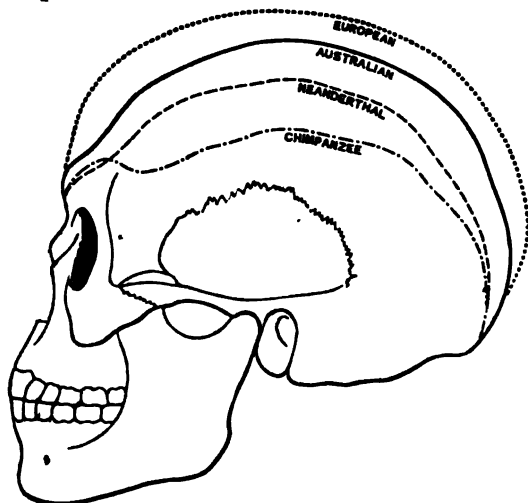


Fig. 2.—Outlines of European, Australian, and Neanderthal Skulls, and that of Chimpanzee. The Australian skull is entire, the dotted lines show the relative degrees of development of the other cranial vaults.

The most important of the race-characters are to be found in the skull. The classification of skulls now generally adopted is that of Retzius, who made two great divisions according to the cephalic index. The *horizontal cephalic index* expresses the ratio between the longitudinal and transverse diameters of the cranium. The former is measured from the central point of the glabella (*ophryon*) to the prominence of the external occipital protuberance (*inion, proboscis*). The greatest transverse diameter of the skull is then compared with the other. If the longitudinal diameter be taken as unity, the transverse varies from .99 to .62. When this ratio is above .80 the skull is said to be *brachycephalic*; when below that figure, it is *dolichocephalic*. The following intermediate forms have been made:—*brachystocephalic* (where the index is .86, or over); *eurycephalic* (.85—.80); *sub-brachycephalic* (.80—.77); *orthocephalic* (.77—.74); *mesocephalic* (.74—.71); *microcephalic* (from .71 downwards) (Huxley). M. Broca has made another classification which we shall give later on.

The following are terms which have been applied to peculiar forms of skulls:—

Acrocephalus, oxycephalus, hypsocephalus, pyrgocephalus, skull of high altitude.

Platycephalus, tapeinocephalus, flattened cranial vault.

Stenocephalus, narrow skull.

Trochocephalus, skull very rounded.

Trigonocephalus, triangular skull—with apex in front, supposed to be due to early synostosis of the medio-frontal suture.

Megalocephalus, skull of very large capacity.

Kephalon, skull thick and large (Virchow).

Microcephalus, leptcephalus, skull very small.

Macrocephalus, large elongated skull.

Plagiocephalus, obliquely oval deformity (Virchow), skull large and flattened in front (Busk).

Cylindrocephalus, elongated cylindrical skull.

Klinocephalus, skull with saddle-shaped vault.

Cymbocephalus, hour-glass skull (this is an exaggeration of the preceding form).

Scaphocephalus, sphencephalus, boat-shaped skull.

Pachycephalus, thick-walled skull.

Those skulls which are well filled all around are distinguished as *crania latiores*; those which present marked depressions between the prominent points are the *crania angustiores* (Cleland).

Another distinctive character of skulls is derived from the proportional development of skull and face. The disproportionate prominence of the lower part of the face, known as *prognathism*, may be due to one of three conditions:—(1) Disproportionate size of the facial bones (*macrognathism*); (2) obliquity of the facial axis to the basicranial, with projection of the maxillæ (true or *maxillary prognathism*); (3) simple obliquity and projection of the upper alveolar arch (*alveolar prognathism*). On a cursory view nothing seems to be more obvious than an estimate of this physical character, which we always do on a profile view of the living head, by dropping an imaginary perpendicular from the root of the nose. If the part cut off in front of this line is considerable, the face is said to be *prognathous*; if not, *orthognathous*. But the attempts to measure the degree of prognathism with mathematical accuracy, has given rise to various and complicated devices, which, however, need not be examined here.

Other important craniological characters to be defined in the skeleton are:—

- (1). The condition of the cranial sutures;
- (2). The prominence of the *inion*.
- (3). The disposition of the *pterion*;
- (4). The part of the face intersected by the anterior production of the occipital plane (plane of foramen magnum).
- (5). The length of the *basio-cranial axis*; i.e., a straight line drawn "from a point midway between the occipital condyles, through the median plane of the skull, to the junction of the ethmoid and pre-sphenoid in the floor of the central cavity." (Huxley).

Great importance is attached by Pruner-Bey to the *harmonic* or *dis-harmonic* proportions of the cranium to the face. A cranium elongated from before backwards, and of proportional elevation, is in harmony with itself; if the face is, at the same time, elongated and narrow, the harmony is complete; this form is

exemplified in the skulls of the Esquimaux and of the Cymri. In the inverse order of harmony we have skulls, such as those of the Lapps and the Auvergnats, which are short, both from before backwards, and from above downwards, while skull and face are both broad from side to side. The famous Cro-Magnon specimen is an example of the dis-harmonic skull; it is elongated from before backwards, while the face is shortened from above downwards. The Tasmanian skull is also of the dis-harmonic type.

The "*coup d'œil*" method of examining the skull came into existence about the same time as craniometry, and was, till recently, much more used. It was introduced by Blumenbach; his method he called the *norma verticalis*. He placed a series of skulls on the ground, "in such a manner that the malar bones were placed in the same horizontal line as was the case when the skulls rested on the lower jaw." He then viewed them successively, with the eye placed directly above the vertex. In this way he saw the general outline and proportions of the skull, and observed the maxillary and zygomatic arches which, in this position, are generally hidden in the white races, but project more or less in the black. About the same date Camper introduced the method of *profile* view. Owen devised the *basic* form of inspection, and Prichard combined all three, and added that of the face. He admitted three fundamental varieties of shape, the *oval*, the *pyramidal*, and the *prognathous*.

Other skeletal peculiarities that have been noticed in races of ancient date and low status, are the perforation of the olecranon fossa, first observed in some skeletons of the Hottentots and Guanches, and since then in the Negro, and in very old European humeri; prominent curvature of the ulna in its upper fourth—directed forwards and inwards; the *fémur à colonne*, *péroné cannelé*, and *plactynemic tibia*.

The *fémur à colonne* is the name given by the French anthropologists to a femur characterised by the presence of a very broad and prominent *linea aspera*, divided into two ridges separated by a rough interval of considerable breadth, and thrown into still greater relief by the excavation of the adjacent parts of the surfaces of the shaft of the bone. The peculiarity

is most strikingly developed in the bones discovered at Cro-magnon.

The *peroné cannelé* is a fibula, characterized by the deeply excavated longitudinal grooves for muscular attachment. The *platynecmic tibia* (*tibia en lame de sabre* of Broca) is so much flattened from side to side as to present but two surfaces and two borders. This peculiarity was first observed in the Cro-magnon bones. It has been since found in a good many specimens of English tibias of the polished stone era.

Of the four forms of outline of the pelvic brim, which were pointed out by *Weber*, the *oval* prevails in the European, the *square* in the Mongolian, the *round* in the American, and the *cuneiform* in the Negro.

Classification of Races.—Of the various attempts that have been made to classify the individuals of the human race, the earliest is that of F. Bernier (1684), who made four varieties—the whites, of Europe; the yellow, of Asia; the dark-coloured, of Africa; and the Lapps, of the North.

The next is that of Linnæus, who made three species of his genus *homo*: *homo sapiens*, *homo ferus*, and *homo monstruosus*. The last includes the microcephalic and plagiocephalic heads of later anthropologists. *Homo ferus* is mute, covered with hair, and his mode of progression is on all fours. *Homo sapiens* comprehends four varieties:—the European, with fair hair, blue eyes, and white skin; the Asiatic, with dark hair, brown eyes, and yellow skin; the African, distinguished by dark and curled hair, dark skin, flat nose, and thick lips; and the American, of tawny colour, dark and long hair, and beardless chin.

Cuvier admitted three distinct races—the Caucasian, the Mongolian, and the Negro. Blumenbach is the originator of the classification which has attained the greatest degree of popularity; he made five varieties, three of which correspond to those of Cuvier, the additional ones being the American and the Malayan. The leading characteristics of these races are as follows:—

I. *Caucasian.*—The skin is fair or slightly brown, always

allowing the colour of the blood to appear; abundant soft, wavy hair, generally of a dark colour; large, orthognathous skull, usually mesocephalic, oval in outline, and symmetrically developed; forehead, lofty and arched; face, and especially the inferior maxillary segment, comparatively small; nose, narrow and straight; lips, thin; teeth, vertical; chin, round and prominent. They inhabit Europe, Arabia, Asia Minor, Persia, Hindostan, and part of America.



Fig. 3.—*Caucasian*.—SIR A. COOPER.

II. *Mongolian*.—This race is characterized by olive skin; dark eyes; black, strong, and straight hair; scanty beard; low forehead; flat and broad face; glabella very wide. The cheek bones are prominent; eyes, oblique with narrow, palpebral fissure, elevated at the outer canthus. Epicanthus often present. The cranium is pyramidal in shape. They inhabit the greater part of Asia and a portion of North America.



Fig. 4.
Epicanthus (after Sir W. Wilde).

III. *Ethiopian*.—The skin is black; the hair black, short, crisp, and woolly; and the sebaceous secretion copious and offensive; the face is markedly prognathous; the skull is dolichocephalic, thick-walled, and of small capacity; forehead, low and retreating; eyes black; nose broad and flat; lips very thick. The arms are markedly long; calf of leg placed high; bones of leg curved; heel project-

ing ; foot flat. They inhabit Africa, Australia, Borneo, and Papua.



Fig. 5.—*Mongolian.*



Fig. 6.—*Ethiopian.*

IV. *American*.—The skin is of a dark red or copper colour ; hair black, soft, and long ; forehead large, but narrow and retreating ; the eyes are large and widely open ; nose, long and aquiline ; lips, thin and delicate. They inhabit America, and are usually known as the American Indians.



Fig. 7.—*Cherokee Skull.*

V. *Malay (Oceanic of Latham)*.—The skin is brown ; hair black and copious ; forehead narrow and rather high ; eyes

black ; eye-lids very widely open ; nose short ; lips thick ; mouth wide ; cheek bones and chin prominent. The skull is brachycephalic, with enormously thick walls and ill-developed frontal sinuses.



Fig. 8.—*Bosjesman playing on the Gourah (Malay).*

Professor Huxley has arranged the different races of mankind in two primary divisions: the *Ulotrichi*, with crisp or woolly hair, and the *Leiotrichi*, with straight hair. The former includes the Negroes and Bushmen of ultra-Saharal Africa, and the Negritos of the Malay Peninsula and Archipelago, and Papuan Islands. The latter are divided into four groups: Australioid, Mongoloid, Xanthocroic, and Melanochroic. The Xanthocroic includes the Slavonians, Teutons, Scandinavians, and the fair Celts. The Melanochroic are the Iberians and dark Celts of Western Europe, and the dark-complexioned whites of the shores of the Mediterranean, Western Asia, and Persia.

Gratiolet has divided the human races into three groups, *frontal*, *parietal*, and *occipital*, according to the region of predominant cerebral development. The first of these corresponds to the Caucasian race, and the last to the Ethiopian, while the second includes the Mongolians with some smaller races.

Very many other modes of classification have been proposed, but it is needless to mention any more.

The following is a list of the horizontal cephalic indices of human races after Broca:—

<i>True Brachycephali.</i>		<i>Sub-Dolichocephali.</i>	
Americans (deformed crania)	1.03	Spanish Basques of Zaraus	} 77
Syrians of G��bel Cheikh (slightly deformed)	.93	Gauls of the Iron Age	
Lapps.	.85	Malgaches	
Bavaria and Swabia	} .84	Chinese	} 76
Auvergnats of St. Nectaire		Copts	
Finns	} .83	Merovingian French	
Indo-China		Slaves of the Danube	
		Tasmanians	
		Polynesians	} 75
<i>Sub-Brachycephali.</i>		Ancient Egyptians	
Alsace and Lorraine	} .82	Guanches	
European Russia		Corsicans of Avepazza (18th century)	
Bretons of the C��tes du Nord (Gaulish Cantons)		Bohemians of Roumania	} 75
Javanese	} .81	Papuans	
Turks		North French (polished stone Age)	
Different Mongols	} .81		<i>True Dolichocephali.</i>
Bretons of the C��tes du Nord (Breton Cantons)		Kabyles	} 74
Estonians	} .80	Arabs	
French Basques		Nubians of Elephantine	
<i>Mesaticephali.</i>		South French of Neolithic Age (from cave Homme-Mort)	} 73
North Americans (undeformed)	} .79	France (Palaeolithic Age)	
South Americans (undeformed)		Negroes of West Africa	
Non-Javanese Malays		Bengalese	} 72
North French (Bronze age)		Kaffirs	
Parisians of 12th, 16th and 19th centuries	} .78	Hottentots and Bosjesmans	
Gallo-Romans		Australians	} 71
Roumanians		New Caledonians	
Mexicans (undeformed)		Esquimaux	

CHAPTER III.

CHEMISTRY OF THE HUMAN BODY.

THE chemical constituents of the human body may be divided, like those of other forms of matter, into elements and compounds. Of the known elements of which the material world is made up, about eighteen have been discovered by physiological chemists in the various solids and fluids of the human framework. But it must not be supposed that they there exist in the uncombined state, as in nearly every instance two or more elements are found united to form chemical compounds of different degrees of complexity. Many of the bases and acids, and of the salts formed by their union, which are found widely distributed throughout inanimate nature, are also found here in considerable proportion; whilst the organic substances of extreme complexity, whose presence is characteristic of the tissues of animal life, require from us a more careful examination. The following is a list of the chemical constituents found in the human body:—

I.—ELEMENTS.

Name.	Symbol.	Atomic Weight.	Present in
Hydrogen ..	H	1	All the tissues and liquids.
Carbon ..	C	12	All the tissues and liquids.
Nitrogen ..	N	14	In a large proportion of the tissues; in solution in the fluids.
Oxygen ..	O	16	In all the tissues; in solution in the fluids.
Sulphur ..	S	32	Albuminous substances; blood; tissue-juices; secretions.
Phosphorus .	P	31	Blood; nervous tissues; bone; teeth; fluids.
Fluorine ..	Fl	19	Bone; teeth; blood (traces).
Chlorine ..	Cl	35.46	All the tissues and fluids.
Silicon ..	Si	28	Hair; blood; bile; urine (traces); epidermis; saliva; bone (?).
Sodium ..	Na	23	Blood; all the secretions; tissue-juices.
Potassium ..	K	39	Muscles; red blood corpuscles; nervous tissues; glands; liver; secretions.
Calcium ..	Ca	40	All the organs, especially bones and teeth; fluids.
Magnesium .	Mg	24	Accompanies calcium.
Lithium ..	Li	7	Muscles; blood; milk (traces found by spectrum analysis).

Name	Symbol.	Atomic Weight.	Present in
Iron ..	Fe	56	Hæmoglobin; bile; urine; chyle; lymph; sweat; milk.
Manganese ..	Mn	55	Accompanies iron—in very minute quantity.
Copper ..	Cu	63.4	Liver and bile.
Lead ..	Pb	207	Accompanies copper (?) } Found but occasionally.

II.—COMPOUNDS.

These are divided into inorganic and organic.

(1).—*Inorganic Compounds.*

This group embraces, besides water, a number of acids, bases, and salts.

(a). WATER. Water is present in every tissue of the body, even the hardest—the enamel of the teeth—possessing a small proportion.

(b). INORGANIC ACIDS.

Hydrochloric HCl In combination with sodium everywhere (nearly); free in gastric juice.

Phosphoric .. H_3PO_4 Bones; teeth; in all the fluids.

Sulphuric .. H_2SO_4 Blood; tissue-juices; secretions; milk.

Hydrofluoric. HF Bones; teeth.

Silicic .. SiO_2 Hair; epidermis; bone; blood; saliva; bile; urine (traces).

(c). INORGANIC BASES.

Soda .. Na_2O Blood; bile; urine; pancreatic juice; secretions.

Potash .. K_2O Muscles; red blood corpuscles; nervous tissues; milk; secretions.

Ammonia .. NH_3 (Traces) blood; urine.

Lime .. CaO Organs, especially bones and teeth; fluids.

Magnesia .. MgO Accompanies lime.

(a). SALTS.

Chloride of sodium .. $NaCl$ All the tissues and fluids of the organism.

„ potassium .. KCl Blood corpuscles; muscles; nervous matter.

„ ammonium .. NH_4Cl In small quantity in the gastric juice, urine, saliva (not constant).

Fluoride of calcium .. $CaFl$ Bones; teeth; blood.

Phosphate of sodium .. $\left\{ \begin{array}{l} Na_2PO_4 \\ Na_2HPO_4 \\ NaH_2PO_4 \end{array} \right\}$ All the tissues and fluids, especially urine and bile.

„ potassium .. $\left\{ \begin{array}{l} K_2PO_4 \\ K_2HPO_4 \\ KH_2PO_4 \end{array} \right\}$ Accompanies phosphate of sodium; abounds especially in red blood corpuscles.

Phosphate of calcium	..	$\left\{ \begin{array}{l} \text{Ca}_3\text{PO}_4 \\ \text{CaHPO}_4 \\ \text{Ca}_2\text{HPO}_4 \end{array} \right\}$	All the tissues and liquids, especially in bones and teeth.
„ magnesium		$\left\{ \begin{array}{l} \text{Mg}_3\text{PO}_4 \\ \text{Mg}_2\text{HPO}_4 \end{array} \right\}$	All the tissues and fluids (traces), especially in the muscles and thymus gland.
„ iron	..	FePO_4	Bile.
Salphate of sodium	..	Na_2SO_4	Most of the tissues and liquids (except milk, bile, and gastric juice).
„ potassium	..	K_2SO_4	Most of the tissues and liquids (except milk, bile, and gastric juice).

(2).—*Organic Compounds.*

The organic compounds are divided into the non-nitrogenous and nitrogenous.

(a). NON-NITROGENOUS COMPOUNDS.

(I). ORGANIC ACIDS.

Of the *Acetic* series—

Formic	..	CH_3O_2	Spleen; muscles; pancreas; thymus; sweat (?); blood in leukaemia; brain; urine.
Acetic	..	$\text{C}_2\text{H}_4\text{O}_2$	Spleen; muscles.
Propionic	..	$\text{C}_3\text{H}_6\text{O}_2$	Sweat; bile; gastric juice (?); urine (?).
Butyric	..	$\text{C}_4\text{H}_8\text{O}_2$	Spleen; muscles; sweat; urine; blood; contents of stomach and intestines; excrements.
Valeric	..	$\text{C}_5\text{H}_{10}\text{O}_2$	Fæces; urine in some pathological conditions.
Capoic	..	$\text{C}_8\text{H}_{16}\text{O}_2$	Sweat; blood; fæces.
Caprylic	..	$\text{C}_8\text{H}_{16}\text{O}_2$	Sweat; blood; fæces.
Capric	..	$\text{C}_{10}\text{H}_{20}\text{O}_2$	Sweat; blood; fæces.
Palmitic	..	$\text{C}_{16}\text{H}_{32}\text{O}_2$	Fat; serum of blood.
Stearic	..	$\text{C}_{18}\text{H}_{36}\text{O}_2$	Fat; serum of blood.

Of the *Glycolic* series—

Carbonic	..	CO_2	Blood and most of the fluids (absorbed as gas); bones; teeth.
Lactic	..	$\text{C}_3\text{H}_6\text{O}_3$	Juice of glands; urine; milk; sweat; gastric juice (?); spleen; thymus; liver; pancreas; thyroid gland; lungs; brain.
Paralactic	..	$\text{C}_3\text{H}_6\text{O}_3$	Muscle juice; liver.

Of the *Oxalic* series—

Oxalic	..	$\text{C}_2\text{H}_2\text{O}_4$	Urine (in form of oxalate of lime); fæces.
Succinic	..	$\text{C}_4\text{H}_6\text{O}_4$	Urine; spleen; thymus; thyroid; blood.

Of the *Oleic* series—

Oleic	..	$\text{C}_{18}\text{H}_{34}\text{O}_2$	Fat; chyle.
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*Sulpho-conjugate Acids.*Phenolsulphuric... $C_6H_5H_7SO_4$ Urine.Chresylsulphuric. $C_8H_9(CH_3)_2SO_4$ Urine.*Acids non-arranged in series.*Cholalic .. $C_{24}H_{40}O_8$ Contents of intestine ; fæces.Choloidic .. $C_{24}H_{38}O_8$ Fæces.Phosphoglycerinic $C_3H_5PO_4$ Nervous matter, and everywhere that lecithin is found (in combination with neurine and the fatty acids).

(II.) ALCOHOLS.

Ethyl alcohol .. C_2H_5O Urine ; milk (Béchamp).Cholesterine .. $C_{26}H_{44}O.H_2O$ Bile ; blood corpuscles ; blood serum ; lymph ; chyle ; nervous tissues ; spleen ; sebaceous matter ; contents of intestine.Glycerine .. $C_3H_5O_3$ Contents of large intestine (traces) ; fats (in combination).Phenol .. C_6H_6O Contents of intestine ; fæces ; urine.

(III.) GLUCOSES.

Glucose .. $C_6H_{12}O_6$ Blood ; chyle ; lymph ; liver ; thymus ; muscles ; urine (?).Muscle Sugar .. $C_6H_{12}O_6$ Muscular tissue (Meissner).Lævulose .. $C_6H_{12}O_6$ Contents of large intestine after ingestion of cane sugar.Inosite .. $C_6H_{12}O_6$ Muscles (especially the heart) ; kidneys ; liver ; lungs ; pancreas ; spleen ; suprarenal capsules ; brain ; spinal cord ; testicles ; blood ; urine.Glycogen .. $(C_6H_{10}O_5)_n$ Liver ; muscles ; white corpuscles ; placenta ; amnion ; many of the tissues and organs of the embryo ; diabetic urine.Dextrin .. $(C_6H_{10}O_5)_n$ Blood ; muscles.

(IV.) SACCHAROSES.

Sugar of Milk .. $C_{12}H_{22}O_{11}$ Milk ; urine (at beginning and end of lactation).

(V.) FATS.

Tripalmitin	.. $C_{51}H_{99}(O.C_{15}H_{31}O)_3$	} Fat ; all the tissues ; all the liquids, except urine.
Tristearin	.. $C_{57}H_{113}(O.C_{18}H_{35}O)_3$	
Triolein	.. $C_{57}H_{103}(O.C_{18}H_{33}O)_3$	

(VI.) SOAPS.

Tripalmitates of soda and of potash	} Blood ; lymph ; chyle ; bile ; contents of large intestine.
Tristearates	
Trioleates	

(VII.) SUBSTANCES DOUBTFUL OR UNCLASSIFIED.

Dyslysin .. $C_{24}H_{36}O_8$ Fæces.Excretin .. $C_{20}H_{30}O(?)$ Fæces.

(d). NITROGENOUS COMPOUNDS.

(I.) ACIDS.

Salphocyanic	..	CNHS	Saliva (of parotid gland).
Carbamic	..	CO ₂ NH ₂	Blood (?).

Uric Acid and its Derivatives.

Uric	..	C ₅ H ₄ N ₄ O ₃	Liver ; spleen ; lungs ; pancreas ; brain ; muscles ; blood ; urine.
Derivatives :—Sarcin		C ₅ H ₄ N ₄ O	Muscles ; spleen ; liver ; suprarenal capsules ; thyroid gland ; marrow of bone ; brain ; kidneys.
„	Xanthin	C ₅ H ₄ N ₄ O ₂	Urine ; liver ; spleen ; pancreas ; thymus ; thyroid ; brain ; muscles ; kidneys.
„	Guanin	C ₅ H ₄ N ₄ O	Pancreas ; liver ; lungs.
„	Carnin	C ₇ H ₈ N ₄ O ₂	Extract of meat.

Alcalamides.

Hippuric acid	C ₉ H ₇ NO ₃	Urine (of herbivora).
Glycocholic..	C ₂₄ H ₄₃ NO ₅	Bile ; urine (traces).
Taurocholic..	C ₂₆ H ₄₅ NSO ₇	Bile ; urine (traces).

Acids not included in series.

Inosic ..	C ₁₀ H ₁₄ N ₄ O ₁₁	Muscle juice.
Cryptophanic	C ₁₀ H ₁₃ N ₂ O ₁₀	Urine.
Paraphanic ..	..	Accompanies the preceding in urine (Thudichum).

(II.) SUBSTANCES ANALOGOUS TO FATS.

Lecithin	..	C ₄₄ H ₉₀ NPO ₈	Nearly all the fluids ; cells during development ; nervous tissues ; spermatozoa ; blood corpuscles.
Protagon (?)	..	C ₄ H ₂ N ₂ PO ₄	Nearly all the fluids ; nervous tissues ; spermatozoa.
Nuclein	..	..	Nervous tissues ; nucleated red corpuscles ; spermatozoa.
Cerebrin	..	C ₁₁ H ₂₂ NO ₃	Nervous tissues.

(III.) AMIDES.

Urea	..	CH ₄ N ₂ O	Urine ; blood ; lymph ; chyle ; transudations ; sweat ; liver ; kidney spleen ; lungs ; brain (?) ; crystalline lens ; vitreous humor ; aqueous humor ; liquor amnii.
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Compound Ureas.

Oxaluric acid	C ₂ H ₂ N ₂ O ₄	Urine.
Allantoin ..	C ₄ H ₆ N ₂ O ₃	Urine; liquor amnii.
Alloxan ..	C ₄ H ₂ N ₂ O ₄	Urine (one specimen); intestinal mucus (one specimen).
Lactic Diamide	C ₃ H ₆ N ₂ O	Urine (Baumstark).

(IV.) AMIDO—ACIDS.

Glycocoll	.. $C_2H_5NO_2$	
Creatin	.. $C_4H_7N_3O_2$	Muscles; nervous tissues; blood; testicle; transudations; liquor amnii.
Leucin	.. $C_6H_{11}NO_2$	Pancreas; spleen; thymus; thyroid; salivary glands; liver; kidneys; suprarenal capsules; nervous tissues; lymphatic glands; contents of the intestine.
Tyrosin	.. $C_9H_{11}NO_2$	Spleen; pancreas (usually accompanies leucine).
Taurin	.. $C_2H_7NSO_2$	Muscles; lungs; fæces.

(V.) AMMONIACAL BASES.

Creatinin	.. $C_4H_7N_3O$	Urine.
Neurin	.. $C_8H_{11}NO_2$	Bile (of ox and pig); exists in licithin.

(VI.) NITROGENOUS SUBSTANCES NOT CONTAINING OXYGEN.

Trimethylamine	.. C_3H_9N	Urine (?).
Napthylamine	.. $C_{10}H_9N$	Fæces.
Indol	.. C_8H_7N	Fæces; contents of intestine.
Scatтол	.. C_8H_9N	Fæces.
Pyrrrol	.. CH_5N	Fæces.

(VII.) SUBSTANCES NOT INCLUDED IN SERIES.

Cystin	.. $C_2H_7NSO_2$	Urine (sometimes); sweat (sometimes); kidneys.
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SALTS.

Carbonate of sodium	.. Na_2CO_3	Blood and urine of herbivora and of omnivora.
„ potassium	.. K_2CO_3	Blood and urine of herbivora and of omnivora.
„ calcium	.. $CaCO_3$	Bones; teeth; oboliths; urine of herbivora.
„ magnesium	.. $MgCO_3$	Urine of herbivora.
Hippurate of sodium	.. $NaC_8H_5NO_3$	Urine of herbivora; urine of man (traces).
„ calcium	.. $Ca_2(C_8H_5NO_3)_2$	Urine of herbivora; urine of man (traces).
Urate of sodium	.. $NaC_5H_3N_4O_6$	Urine; blood; spleen; liver; pancreas; lungs; brain.
„ potassium	.. $KC_5H_3N_4O_6$	Urine; blood; spleen; liver; pancreas; lungs; brain.
Oxalate of calcium	.. CaC_2O_4	Urine (sediments).
Glycocholate of sodium	.. $NaC_{24}H_{43}NO_6$	Bile.
Taurocholate of sodium	.. $NaC_{25}H_{44}NSO_6$	Bile.
Sulphocyanide of potassium	.. $KCyS$	Saliva of parotid gland; milk (?).
„ sodium	.. $NaCyS$	Saliva of parotid gland; milk (?).
Phenosulphate of potassium	.. $C_6H_5K_2SO_4$	Urine (Baumann).

PIGMENTS.

Hæmoglobin	..	$C_{600}H_{860}N_{154}FeS_3O_{179}$	Blood.
Hæmatin	..	$C_{34}H_{34}N_4FeO_5$	Blood.
Bilirubin	..	$C_{18}H_{16}N_2O_3$	Bile.
Biliverdin	..	$C_{16}H_{20}N_2O_5$	Bile ; fæces.
Indican	..	$C_{26}H_{31}NO_{17}$	Urine ; sweat.
Urobilin	..	$C_{32}H_{40}N_4O_7$	Urine.
Lutein	..	?	Vitellus ; corpus luteum ; coloring matter of fat and of serum.
Melanin	..	?	Pigment.

ALBUMINOUS SUBSTANCES.

A.—A. S. PROPERLY SO CALLED.

I.—ALBUMENS.

1. Albumen of serum .. Blood serum ; lymph ; chyle ; milk (at commencement of lactation) ; colostrum ; crystalline lens ; transudations ; urine (of albuminuria).
2. Albumen of egg .. White of egg.

II.—GLOBULINS.

1. Vitelline .. Crystalline lens ; yolk of egg.
2. Myosin .. Muscle-plasma ; nervous tissues ; cornea.
3. Paraglobulin .. Blood-corpuscles ; plasma ; cornea ; connective tissues.
4. Fibrinogen .. Blood-serum ; transudations.

III.—FIBRIN.

- Fibrin .. Blood-clot ; chyle ; lymph ; transudations.

IV.—PROTEINS.

1. Casein .. Milk.
2. Alkali-albuminate .. Blood corpuscles ; plasma ; chyle ; crystalline lens ; cornea ; muscles ; nervous tissues ; growing cells ; pancreas.
3. Syntonin .. Contents of stomach during digestion.

V.—PEPTONES.

1. Peptones of Albuminoids.
2. Peptones of Gelatine.

VI.—CRYSTALLINE ALBUMINOIDS.

1. Hæmoglobin .. Red blood corpuscles ; muscles.
2. Vitelline Plates .. Vitellus of fishes.

VII.—SOLUBLE FERMENTS.

1. Ptyalin .. Saliva ; pancreatic juice.
2. Pepsin .. Gastric juice.
3. Trypsin .. Pancreatic juice.
4. Inversive Ferment .. Intestinal juice.
5. Ferment of Fats .. Pancreatic juice.
6. Fibrin-ferment .. Plasma of blood.

B.—DERIVED ALBUMINOIDS.

I.—CHEMICAL DERIVATIVES.

1. Paralbumin .. Certain transudations.
2. Colloid substance .. Ovarian cysts; goitre.
3. Amyloid substance (lardacein) Amyloid degeneration of organs.
4. Mucin .. Submaxillary saliva; mucus secretions.
5. Nuclein (?) .. Spermatozoa; pus-corpuscles.
6. Spermatin .. Semen.

II.—HISTOGENETIC DERIVATIVES.

1. Collagenous substance and gluten .. Connective tissue.
2. Collagenous substance Connective tissue.
3. Chondrogenic substance and chondrin Cartilage; cornea.
4. Elastin Elastic tissue.
5. Keratin Epidermis, and epidermic structures (hairs, nails, epithelium, horny tissue, &c.

Of the elementary constituents of the human body which have been enumerated, the first four—carbon, hydrogen, oxygen, and nitrogen—are of pre-eminent importance, and accordingly are known as the *essential* elements, while the metallic elements, which close the list, are so uncertain in appearance, and, apparently, so unnecessary to the animal economy as to be denominated *accidental*.

GASES.

The following table, from Volkmann, gives the per-centage of water, carbon, hydrogen, nitrogen, and of ash in the principal organs of the human body:—

		H ₂ O	C	H	N	O	Ash.
Skeleton	..	50.	18.06	2.74	2.3	4.78	22.11
Muscles	..	77.	11.73	1.71	3.04	5.47	1.05
Heart	..	79.3	10.96	1.6	2.5	4.58	1.06
Brain	..	77.9	12.62	1.93	1.37	4.41	1.41
Fatty Tissue	..	15.	64.78	10.1	.45	9.67	—
Lungs	..	79.14	10.7	1.46	2.52	5.01	1.16
Liver	..	69.6	15.88	2.25	3.09	7.79	1.38
Spleen	..	76.59	12.13	1.78	3.01	4.99	1.5
Alimentary Canal	..	77.98	11.7	1.54	2.87	4.88	1.07
Kidneys	..	83.45	8.73	1.29	1.93	3.8	.8
Skin	..	70.	14.6	2.12	3.64	8.93	.7
Pancreas	..	78	11.13	1.92	2.11	5.97	1.05
Blood	..	79	11.53	1.34	2.99	4.28	.85
Rest of Body	..	76.35	12.13	1.74	3.01	5.73	1.03
Mean	..	65.7	18.15	2.7	2.6	6.5	4.7

The gases of the human body are oxygen, carbonic acid gas, hydrogen, nitrogen, carburetted hydrogen, and sulphuretted hydrogen. These are found in three different states:—(1) free, in certain cavities (alimentary canal and respiratory passages); (2) in solution in the different fluids; (3) in chemical combination.

Oxygen. O.—This gas exists—(1) in the free state in the respiratory passages and in the alimentary canal. In the former situation it is part of the inspired air; in the latter, it is swallowed with food and drink. (2) In solution, oxygen is found in nearly all the fluids of the human body, especially in the liquor sanguinis. In bile and urine its presence has not been ascertained. In this state oxygen follows the so-called Henry-Dalton law of the absorption of gases.

(3) Oxygen is found in a state of loose combination with the hæmoglobin of the red blood corpuscles forming oxy-hæmoglobin.

The functional importance of oxygen depends on its affinity for organic substances. By combining with the latter in different ways the various species of oxidation are carried on, from which result the production of heat, muscular contraction, phenomena of innervation, and the other vital forces of the animal frame. Still the theory of the direct combustion of the various substances of the animal organism by oxygen, on which all vital phenomena had been supposed to depend, has lost ground within the last few years, and is now almost entirely supplanted by the fermentation hypothesis, according to which the rôle of oxygen is rather that of a stimulus than of an agent of direct oxidation. We shall return to this question again.

Carbonic Acid Gas. CO_2 .—This gas, like the one last mentioned, is found (1) in a free state in the lungs and in the alimentary canal. The percentages given by Chevreul are—small intestine, 24.39–40.25; large intestine, 43.5–70; cæcum, 12.5; rectum, 42.86. In the lungs it is derived from the chemical changes which take place in the blood and tissues. In the intestine, partly from a similar source, but chiefly from decomposition of the contents of the alimentary canal. The proportion of CO_2 in atmospheric air is so small that it may be disregarded as a source in either case.

(2) In a state of simple solution CO_2 is generally believed to exist in all the fluids of the body. This has, however, been

contradicted by Bert, who asserts that it is all in a state of combination, and indeed the result of most recent researches would seem to indicate the existence of the CO_2 in great part in union with alkalies as carbonates and phospho-carbonates. This would be (3) a third form of the existence of the gas.

CO_2 is one of the ultimate products of the chemical changes which are always taking place in the tissues and fluids, and is eliminated from the system, chiefly by the lungs, and in smaller quantity by the skin and alimentary canal, the quantity daily expelled being—from the former about 900 grms. (30 oz.), from the latter about 4—10 grms. (.0133—.33 oz.).

Nitrogen. N.—Nitrogen is found, like oxygen, (1) in the free state in the lungs and in the alimentary canal, derived from the air, inspired or swallowed, as the case may be. Chevreul found the following per-centages :—in the stomach, 71.45 ; small intestine, 20.8—8.85—66.6 ; coecum, 67.5 ; colon, 51.03—18.4 ; rectum, 45.9. The quantity in the large intestine is increased after eating meat (Ruge), and being usually greater than that in the small intestine, would point to some other source than the atmospheric air.

(2) In the state of solution, N is found in small quantity in all the fluids, where it is derived from the inspired air ; a minute proportion perhaps being derived from metamorphosis of the nitrogenous tissues. It is eliminated from the same parts as the CO_2 .

Hydrogen.—H is found (1) in the free state in the expired air (a very small proportion), and in considerable quantity in the alimentary canal. According to Chevreul the gases of the stomach contain 3.55 per cent. of free H ; of the small intestine, 5.4—11.6 ; of the large, 7.5. Other chemists deny the existence of free H in the stomach. The proportion in the large intestine is greatest after milky food ; least after meat. The source is probably a butyric fermentation. From the alimentary canal it passes into the blood, and thence into the expired air, and (according to Pettenkofer) into the cutaneous perspiration.

(2) In a state of solution, H has been found in venous blood, the probable source being from the alimentary canal. It is also found in pus.

Carburetted Hydrogen. CH_4 .—This gas is found in a free state in the large intestine, of which it forms about 5.5—11.2

per cent. of the contained gases. Its presence is due to chemical changes in the ingesta. It has been found in the expired air by Regnault.

Sulphuretted Hydrogen. H_2S .—This gas is found in small quantity in the alimentary canal, especially when taking animal food. Its source is the decomposition of the proteids, and their sulphur-holding derivatives (*e.g.*, from some of the constituents of the bile). The following table gives the gases of the principal fluids of the body, with the number of volumes per hundred vols. of the containing liquid (from Beaunis):—

	Arterial Blood.	Venous Blood.	Arterial Serum.	Lymph.	Acetic Fluid.	Milk.	2 Bile of Dog.	3 Bile of Dog.	Saliva of Dog.	Urine.	Muscle-juce.	Egg-albumin.	Pus.
CO_2	50	60	50	45.9	142.	10.	7.36	73.81	74.93	18.09	15.4	66.76	75.28
N	..	..	..	1.67	21.1	1.05	.78	.52	.92	1.21	4.9	3.77	2.50
O	20	10	1.47	.13	.24	.11	..	.26	.65	.1	.09	2.31	..
H	..	..	..	..	..	..	..	..	..	..	..	..	5.16
Total	72	72	63.47	48.70	163.24	11.16	8.14	74.59	76.50	19.40	19.39	72.84	82.94

Water.—Water is found in the human body in three states:—

(1) As a menstruum of substances dissolved or suspended: as such it forms the greater part of the fluids, blood, lymph, chyle, &c.

(2) As water of imbibition, it enters into the formation of the various tissues of the body.

(3) As water of combination, it enters into the chemical formation of many of the organic substances of the organism, corresponding to the water of crystallisation of less complex forms of matter. Besides the quantity of water introduced by food and drink, there is no doubt that some is formed by chemical changes in the system: water and carbonic acid gas being the latest forms of oxidation of organic substances.

Water forms about two-thirds of the whole weight of the body. The following table gives the amount per 1000 present in the chief constituents of the human organism:—

Enamel	...	...	2	Cartilage	..	..	505
Dentine	...	...	100	Liver	...	...	693
Skeleton	...	...	486	Spinal Cord	...	...	697
Fat	...	...	299	Skin	...	...	720
Elastic Tissue	...	...	496	Brain	...	...	750

{ Grey matter of Brain	858	Plasma	...	...	901
{ White " " ...	700	Chyle	...	...	928
Muscles	...	Lymph	...	...	958
Spleen	...	Serum	...	...	959
Thymus	...	Gastric juice	...	...	973
Connective tissue	...	Intestinal juice	...	...	975
Kidneys	...	Tears	...	...	982
Vitreous humor	...	Aqueous humor	...	...	986
Blood	...	Cerebro-spinal fluid	...	...	988
Bile	...	Saliva	...	...	995
Milk	...	Sweat	...	...	995
	891				

The elimination of water from the system is carried on by the kidneys, the skin, the lungs, the intestine, and the quantity so eliminated is found to correspond pretty closely with that introduced into the system.

MINERAL SUBSTANCES.

All the tissues and fluids of the body, without exception, contain a certain proportion of mineral salts. The following table gives the proportion present in the principal organs and liquids of the human organism :—

Enamel	..	..	964.1	Von Bibra.
Dentine	..	...	719.9	—
Bone	..	..	654.4	Zalesky.
Cartilage	..	..	31.	Fromberz and Gugert.
Muscle	..	..	15.4	(a mean taken from many analyses.)
Elastic tissue	..	..	11.8	Schultze.
Liver	..	..	11.03	Oidtmann.
Yolk of egg	..	..	9.65	Gobley.
Pancreas (old woman)	..	..	9.5	Oidtmann.
Cornea	..	..	9.5	His.
Vitreous humor	..	..	8.8	Lormeyer.
Crystalline lens	..	..	8.2	Laptschinsky.
Blood corpuscles	..	..	7.28	C. Schmidt.
Kidney (infant of 14 days)	..	..	7.	Oidtmann.
Egg-albumen	..	..	6.6	Lehmann.
Brain	..	..	5.12	Geoghegan.
Spleen	..	..	4.94	Oidtmann.
Hair (of blonde)	..	..	4.74	Baudimont.
Pancreas (infant of 14 days)	..	..	3.7	Oidtmann.
Hair (dark-coloured)	..	..	2.58	Baudimont.
Kidney (old woman)	..	..	.99	Oidtmann.

Sodium and Sodium Salts.—The chloride of sodium is found in all the tissues and fluids of the body, especially abounding in

liquor sanguinis, lymph, bile, pancreatic juice, and urine. It has been estimated that about 200 grms. (6.6 oz.) of this salt exist in the human body. The following table gives the quantities of chloride of sodium and chloride of potassium present (per 1000), in the most important of the fluids of the body.

					NaCl.	KCl.
Blood	..	..	..	..	2.7	2.05
Corpuscles	..	..	..	..	..	3.67
Plasma	..	..	..	..	5.54	.35
Lymph	..	..	..	..	5.67	—
Chyle	..	..	..	..	5.84	—
Gastric juice	..	..	..	..	1.45	0.55
Pancreatic juice (permanent fistula)	..	..	..	..	2.5	.93
" " (temporary fistula)	..	..	..	..	7.35	.02
Bile	..	..	..	..	5.53	.28
Milk	..	..	..	..	.87	2.13
Urine	..	..	..	..	11.	4.5

The chloride of sodium is entirely derived from the ingesta. The great bulk is again eliminated chiefly by the kidneys, and in small quantity from the alimentary canal, skin, salivary glands, and nasal mucous membrane. But a certain quantity is decomposed in the system, and from this source chlorine is supplied to the chloride of potassium of the red blood corpuscles and of muscular fibre, and also to the hydrochloric acid of the gastric juice. The sodium of the bile salts also is derived from the same source. When chloride of sodium is withheld from an animal the blood and tissues still continue to retain it with peculiar tenacity. Ingestion of large quantities of chloride of sodium increases the amount of urea excreted, and also increases the watery constituents of the urine, apart from the necessary augmentation produced by the large quantity of fluid taken under the influence of thirst.

The presence of sodium seems to be of great importance in promoting diffusion of liquids in the various parts of the body. If albumen is injected into the rectum of an animal it is not absorbed, but will rapidly be if some chloride of sodium has been previously added. If an endosmometer containing a concentrated solution of common salt be plunged into water, it rapidly attracts a large quantity of the water, and this experiment furnishes the probable explanation of the action of saline purgatives.

Potassium and Potassium Salts.—The chloride of potassium

accompanies nearly everywhere the chloride of sodium. But the sodium salts predominate in the liquids, while the solid organs, and more especially the highly organised tissues, are notably rich in salts of potassium. Experiments have shown that the absence of potassium salts from the food causes great emaciation. Taken internally, in small quantities, they have the effect of quickening and strengthening the heart's action, and increasing the blood-pressure. According to some high authorities the stimulating action of tea, coffee, broths, extract of meat, &c., is due to the presence of potassium salts.

The salts of potassium and sodium, especially the alkaline salts of the blood, are supposed to fulfil an important function in the animal economy by promoting oxidation to a powerful degree. The reaction of Barreswill is an example of an organic substance giving no chemical result under ordinary conditions, but undergoing rapid oxidation in presence of an alkali. Magawly and Piotrowski have shown that the free organic acids, when introduced into the system, pass into the urine unchanged, but when combined with potassium and sodium, to form alkaline salts, they undergo rapid oxidation.

The presence of alkalies is also necessary for the saponification of fats.

Ammonia and Ammonia Salts.—The presence of ammonia in urine has been demonstrated by Heintz, Boussingault, and Neubauer. About 0.7 grm. is in this way cast off from the system per diem. It is probably combined with phosphate of soda. The ingestion of acids increases the quantity of ammonia in urine (Schmiedeberg and Walter), whilst in the experiment of making the urine of a carnivorous animal (dog) alkaline, by the exclusive use of a vegetable diet, the quantity of ammonia was found gradually to diminish (Salkowsky and Munk).

Small quantities of ammonia are also found in urine, sweat, gastric juice, blood, and in the expired air. It has been supposed that the ammonia found in these various situations is derived from the decomposition of urea, of which a small portion may find its way into the alimentary canal with the digestive juices, and having there become decomposed, the resulting ammonia is taken up by the blood.

Calcium Salts.—Those which have been found in the human

body are—the fluoride, phosphate, carbonate, sulphate, oxalate, and urate.

The *fluoride* of calcium is found in the bones, and in large quantity in the enamel of the teeth, and minute traces have been found in the blood, in milk, and in the substance of the brain (Wilson, Horford).

The *phosphate* of calcium is present in almost all the tissues and in all the fluids. Every tissue of the body, excepting the elastic, leaves on incineration a residue chiefly consisting of phosphate of calcium, hence it is believed to be chemically united to the proteid substances, as well as existing in a state of simple solution in the liquids of the tissues. It is also dissolved in the urine of carnivora, and more especially of man; in the urine of herbivora it is merely in a state of suspension, but in very small quantity.

Carbonate of calcium is found in the otoliths of the internal ear, and accompanies the phosphate in bone, teeth, and some other tissues.

Sulphate of calcium has been found by some observers in bone, also in the blood and in the pancreatic juice. Urate and oxalate have been found only in urinary deposits (always in the solid form). Elimination of calcium salts is performed partly by the kidneys, partly by the alimentary canal. A remarkable distinction in this respect exists between the carnivora and the herbivora; in the former the elimination is chiefly by the alimentary canal, in the latter by the urine; in the case of the former the phosphates predominate, in the latter the carbonates.

The presence of lime salts is necessary to give solidity to the tissues, especially the osseous, and cases of softening of the bones have been found to follow their prolonged abstraction from the food (*inanition minérale* of Dusart).

Magnesium Salts.—The *phosphate* of magnesium accompanies the phosphate of calcium nearly everywhere, but in very small proportion, excepting in the muscles and in the thymus gland, where the quantity is larger than that of the phosphate of calcium (Gorup-Besanez). The elimination of magnesium salts is exactly similar to that of the calcium salts which they accompany.

Iron.—This metal is found especially in the blood—in the red corpuscles—where it enters into the formation of the

hæmoglobin. This view has been contradicted by Paquelin and by Joly, who assert that hæmoglobin contains no iron, and that the latter exists in the corpuscles in the state of a tribasic phosphate. Small quantities of iron have also been found in chyle, lymph, bile, milk, urine, gastric juice (in form of chloride), in the pigment of the eye and in hairs. All the vascular organs contain some. The spleen has the largest proportion, greater even than that of the blood itself, and is, according to Picard, a reservoir of iron for the system.

Iron is taken into the system with the food, chiefly in form of phosphate, and is eliminated with the fæces as a sulphate of the metal.

Manganese.—This accompanies iron in the body as it does nearly everywhere in nature. It has been found in the blood, and also in bile, and in hairs.

Copper, Lead, Zinc.—These metals have been found in the liver and sometimes in blood and bile in minute quantities, but their presence is probably in every case purely accidental.

Hydrochloric Acid.—This acid exists in the free state only in the gastric juice. It is here derived from the chloride of sodium of the gastric glands which is decomposed in the act of secretion, and after having fulfilled its purposes in digestion it recombines with the sodium (of the bile or of the food) in the alimentary canal, and in great part passes into the blood again as chloride of sodium.

Phosphoric Acid.—This acid is found in three important organic compounds of the body—lecithin, nuclein, and phosphoglyceric acid. According to Hoppe-Seyler the proteids do not contain phosphorus, and its apparent existence is due to the great difficulty of removing lecithin and nuclein completely from the proteids.

The principal phosphates found in the system are as follows :—

Phosphate of Sodium	..	..	Na_3PO_4 : Na_2HPO_4 : NaH_2PO_4 .
„ Potassium	..	..	K_3PO_4 : K_2HPO_4 : KH_2PO_4 .
„ Calcium	..	..	Ca_3PO_4 : CaH_2PO_4 .
„ Magnesium	..	..	Mg_3PO_4 .
„ Ammonia and Magnesia			$\text{NH}_4\text{Mg}_2\text{PO}_4 \cdot 6\text{H}_2\text{O}$.

The phosphates are introduced into the system with the food, and eliminated with the urine and the fæces. The urine of 24 hours contains 2.5—3.5 grms. of phosphoric acid.

The physiological importance of the phosphates is very great. The alkaline phosphates, especially that of soda, contribute to maintain the alkalinity of the blood, and promote (as has been shown by Liebig and by Frerichs) the solution of the albuminoids, and the phenomena of diffusion. They also influence the absorption of carbonic acid gas by the blood, and maintain the solution of any urates and oxalates which are present.

Carbonates.—The ash of nearly every tissue contains the alkaline carbonates, but the carbonic acid comes, in most instances at least, from the decomposition of the organic acids of these substances. The carbonic acid is introduced into the system by the food, either directly as such, or indirectly as arising from the decomposition of the vegetable acids, citric, malic, &c. Carbonic acid gas is also formed in the system, being as already observed, one of the final products of oxidation of albuminoid matters, and is derived from the decomposition of certain organic acids (such as lactic) which are formed in the system. The elimination is chiefly by the kidneys.

The alkaline carbonates favor diffusion and maintain the solution of proteids in the blood and other fluids, as already mentioned.

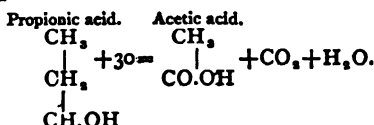
Sulphur and Sulphates.—Sulphur is one of the formative elements of all proteids. Alkaline sulphates are found in the blood, and in most of the tissues and fluids of the organism, the prominent exceptions being milk, bile, and gastric juice. The sulphur is derived chiefly from that of the food; partly from the oxidation of that of the proteids. The use of a diet rich in albuminoids has been found to increase the sulphates of the urine (Vogel, Clare, Bence Jones); and it has also been demonstrated that elimination of sulphur by the kidneys is found to vary directly as that of the urea. Sulphur is chiefly eliminated with the urine, but in small quantity also with the fæces. The daily amount excreted by the kidneys is about 1.5—2.5 grms., and according to the calculations of Kunkel it amounts to 60 or 70 per cent. of the quantity taken into the system with the albuminoids of the food. A small quantity is found here in the form of phenol-sulphuric acid, whilst a part of that eliminated by the alimentary canal is in the form of sulphuretted hydrogen, the solid part being chiefly a sulphate of iron.

ORGANIC COMPOUNDS.

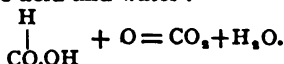
(a) NON-NITROGENOUS.

(I.) ORGANIC ACIDS.

ACETIC ACID SERIES.—Formula $C_nH_{2n}O_2$.—These acids are all monatomic and monobasic; and, as shown by the general formula, each contains two atoms of oxygen and twice as many atoms of hydrogen as of carbon. They are all formed by the union of a radical of alcohol with the group of atoms CHO_2 (hydrate of carboxyle). As shown by the table on a preceding page, most of the acids of this series have been found in the liquids of the human body, especially in blood, bile and urine, but always in small proportion. The highest of the series, palmitic, margaric, and stearic, enter into the formation of fats. The so-called margaric acid appears to be a simple mixture of palmitic, and stearic acids (Beaunis). The acids of this series are produced by oxidation of the organic acids, of hydrocarbons, fats, proteids and certain nitrogenous substances, such as glycocoll, and more particularly leucin. Each can be derived from that immediately following it in the series by the oxidation of the latter, of which an example is represented by the following equation:—



And the first of the series, formic acid, is converted by oxidation into carbonic acid and water:—

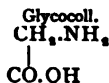
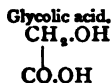


Such is probably the final stage to which all the acids of this series are reduced before elimination.

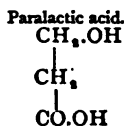
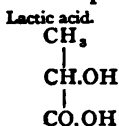
The fatty acids are often, at least, produced, not by oxidation, but by fermentation, as is shown in the action of the pancreatic juice upon fats, by which they are decomposed into the corresponding fatty acids and glycerine. A certain proportion of the volatile fatty acids, especially acetic and butyric, are eliminated with the fæces without having undergone decomposition, and small quantities of palmitic and stearic acids are also found there in the form of soaps.

ACIDS OF THE GLYCOLIC SERIES.—Formula, $C_nH_mO_p$.—These acids differ from the corresponding ones of the acetic series only in the possession of an additional atom of oxygen, and are formed respectively from the latter by replacing an atom of the hydrogen of the alcoholic radical by the hydroxyl radical HO. These acids are diatomic and monobasic. Those of greatest physiological importance are the glycolic, lactic, and leucic acids.

Glycolic (oxy-acetic) Acid does not exist in the human body, but is intimately related with a very important constituent, glycoll. The latter body differs from the acid named in the substitution of the radical NH_2 for the hydroxyl radical HO of the acid.



Lactic Acid is found in two isomeric forms: the ordinary lactic acid, and the paralactic.

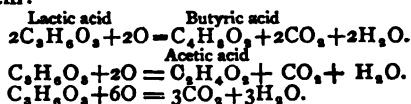


Both these forms occur in the human body. The usual situations have been enumerated in the table given above. The occurrence of the paralactic acid in muscular tissue (both smooth and striated) has given origin to the name *sarcolactic*, but the acid distinguished by the latter name is merely a mixture of paralactic acid with a very small quantity of ordinary lactic acid (Wislicenus). Paralactic acid has also been found in leucocythemic blood, in pus, and sometimes in ovarian cysts.

In most situations lactic acid exists in combination as an alkaline lactate, but it occurs in the free state in gastric juice, and probably in muscular tissue. There are two great sources of this acid: (1) it is formed in the intestines by fermentation of the saccharine constituents of the ingesta; (2) it is formed in the tissues, especially the muscular, and at the expense, partly of the glycogen, and partly of the hydrocarbons contained in the muscle.

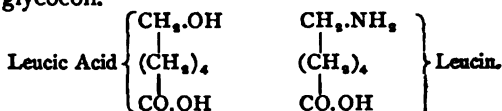
Lactic acid is not eliminated as such, but by oxidation gives rise to the formation of sundry intermediate products, and is

finally discharged, at least in great part, in the form of carbonic acid and water. The following chemical equations represent some of the possible oxidations which lactic acid may undergo in the system:—



Some of the lactic acid of the intestine probably undergoes fermentation, giving rise to the formation of butyric and propionic acids—carbonic acid and hydrogen being set free.

Leucic (oxy-caproic) Acid.— $\text{C}_6\text{H}_{11}\text{O}_3$. This acid does not exist in the human body, but it has the same relation to leucin, a substance of great importance in the body, that glycollic acid has to glycocoll.



OXALIC ACID SERIES.—Formula $(\text{C}_n\text{H}_{2n})_2\text{O}_4$.—These acids are diatomic and monobasic, and are derived by oxidation from the volatile fatty acids and from the acids of the glycolic series.

Oxalic Acid.— $\text{C}_2\text{H}_2\text{O}_4$.—This acid is found in the urine, mostly during the use of vegetable food, and especially after the ingestion of sorrel, of effervescing liquors, beer, wine, &c. It occurs in the form of oxalate of calcium and is maintained in solution by the acid phosphate of sodium. A larger quantity is found in the urine of the herbivora.

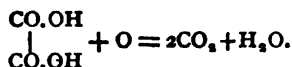
The sources of oxalic acid are two: (1) From food; and in addition to the aliments already mentioned it has been found that certain organic acids, such as citric, give rise to the formation of oxalic acid (H. Müller, Kölliker); (2) It can be formed in the system by the oxidation of many organic substances, nitrogenous and non-nitrogenous: proteids, fats, hydrocarbons, volatile fatty acids, glycerine, uric acid, &c. Wohler and Frerichs have found that the injection of uric acid or urates into the blood increases the amount of oxalate of calcium in the urine. Schunk has endeavoured to show that the oxalic acid of the urine is derived from oxaluric acid, which is changed into oxalic acid and urea, but his hypothesis has not met with

any favour. Engel has endeavoured to prove that glycoll is eliminated in the form of oxalic acid, but his experiments have been shown to be entirely fallacious. Drechsel has succeeded in making oxalate of sodium by synthetical combina-

tion of sodium and carbonic acid: $2\text{CO} + 2\text{Na} = \begin{array}{c} \text{CO.ONa} \\ | \\ \text{CO.ONa} \end{array}$

and it is supposed that in a similar way must be explained the formation of oxalates in the system which follows the injection of effervescing drinks.

Part of the oxalic acid is eliminated in the state of oxalate of calcium by the kidneys. But a much larger proportion is decomposed and forms carbonic acid and water.



Succinic Acid. $\text{C}_4\text{H}_6\text{O}_4$.—This acid is found in small quantity in the urine, especially after the ingestion of aliments containing organic acids, particularly malic. It has been found in the saliva, sweat, and urine after the ingestion of benzoic acid (Meissner and Sheppard). Its presence has also been demonstrated, under ordinary circumstances, in the spleen-pulp, thymus, thyroid, and in a certain number of pathological products. Succinic acid is also a product of the decomposition of albuminoids, especially of casein, of the oxidation of fats, and also of the alcoholic fermentation.

Like the last-mentioned acid, it is, probably in every instance, reduced before final discharge from the system, into carbonic acid and water. This transformation is sometimes direct; more usually intermediate products are previously formed.

OLEIC ACID SERIES.—Formula, $\text{C}_n\text{H}_{2n-2}\text{O}_2$.—The acids of this series correspond to the volatile fatty acids of the acetic group; two atoms of H in the latter being replaced by an atom of O of the group CO.OH.

The only acid of this series found in the human organism is the oleic, which exists under conditions nearly similar to those of the stearic acid already spoken of as a constituent of neutral fats and soaps. Very small quantities are found in the free state in the blood, in bile, in certain pathological fluids, and in larger proportion in the contents of the intestine and in the feces. In all these situations its presence is due to the de-

composition of the corresponding neutral fat. Oleic acid in its turn is decomposed into sebacic acid, carbonic acid, and carburetted hydrogen. By the action of potash it is found to produce acetic and palmitic acids. All these products are found in each of the different excretions.

ALCOHOLS.

Three alcohols are found among the constituents of the human organism; two of these are monatomic, the ordinary ethyl alcohol and cholesterin; the third is glycerine, one of the triatomic group.

Ethyl Alcohol, C_2H_5O .—Alcohol is always found in quantity in the urine, and also in the blood and tissues of the body after the ingestion of alcoholic beverages of any kind. But according to some authorities (Bechamp and Rajewski), alcohol is a normal constituent of the human body, and exists independently of the imbibition of fermented liquors. If this be true, it would point to the destruction of part of the glucose formed in the system otherwise than by oxidation—by alcoholic fermentation.

Alcohol introduced into the system is partly eliminated as such by the lungs, the kidneys, and the skin; a portion is oxidised in the blood, and forms carbonic acid and water.

Cholesterin, $C_{27}H_{44}O.H_2O$ (Latschinoff).—The exact chemical constitution of cholesterin is not definitely settled. It is the richest in carbon of all the non-nitrogenous organic compounds. It was long believed that cholesterine was peculiar to the animal kingdom, but recent researches have demonstrated its presence in certain plants, especially in the grains of the cereals, peas, beans, lentils, &c.

In the human organism, cholesterin is found in bile, dissolved by the salts of the biliary acids, in the serum of the blood, in transudations, and in some pathological fluids. It is also found in blood corpuscles, in the nervous tissue of the brain and spinal cord, and in the spleen, in which situations it appears to be associated with lecithin.

The origin of this substance is very obscure. Miahle endeavoured to prove that it was derived from decomposition of the proteids, but completely failed to establish his theory. Flint tried to show that it was produced by metamorphosis of the cerebral substance; his analyses have also proved to be fallacious. The seat of its formation, and its physiological importance, are

equally obscure. There is no doubt, however, that the quantity of cholesterin is always increased by anything that causes marked retardation of the process of oxidation, whether in an organ, or in the entire system.

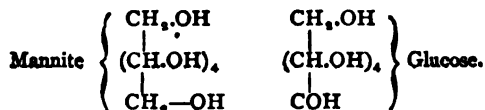
Glycerine, $C_3H_5O_3$.—This compound is a triatomic alcohol, formed by the union of the triatomic alcohol radical C_3H_5 , with three of the hydroxyle OH. In combination, it enters into the formation of neutral fats, which are the ethers of glycerine. In the small intestine it is set free by the action of the pancreatic juice, and its subsequent fate still remains a disputed matter. Some believe that it is absorbed as such, and rapidly changed in the blood; others maintain that it is changed in the digestive tube itself. If the former idea be founded on fact, the glycerine must, after absorption, undergo extremely rapid metamorphosis, for it has not been found in a free state in the blood. The experiments of Scheremetjewski and Catillon have demonstrated the extreme rapidity with which glycerine disappears when injected into a blood vessel; the only demonstrable result being an almost immediate increase in the amount of CO_2 expired, and the carbon of the same was found to agree in quantity with that of the glycerine injected: the explanation of this would be a rapid and complete oxidation of the glycerine in the blood with the formation of carbonic acid and water. Another view is that advocated by Van Deen, and others, who found that the introduction of glycerine into the stomach was followed by a corresponding increase of the hepatic glycogen, and accordingly the last-named authority concludes that the glycogen is entirely formed directly from the glycerine absorbed in the intestine. Against this view, however, we have the evidence of Pink, who has shown that the injection of glycerine into a mesenteric vein does not increase the amount of hepatic glycogen, more than would the introduction of a corresponding quantity into the subcutaneous areolar tissue, so that the influence of glycerine on the glycogenic substance of the liver is probably only indirect, and may be, as suggested by Beaunis, due to the fact that the glycerine, by its affinity for oxygen, prevents the oxidation of other substances which go to form the hepatic glycogen. Plosz has found in the urine of animals, after ingestion of glycerine, a substance analogous to glucose, but without any tendency to ferment, and having no influence on polarised light. He believes it to be an aldehyd of glycerine. The experience

of Berthelot is in favour of the change of glycerine into glucose. He has obtained the latter substance by rubbing up together testicular tissue and glycerine.

The second idea of the fate of the free glycerine of the small intestines, is that it is changed or eliminated by the intestine itself, but no account of even moderate plausibility has been given by the advocates of this view. Beneke believes that phosphoric acid which is set free in the stomach during digestion, by the action of the hydrochloric acid on the alkaline phosphates of the food, combine with the glycerine in the small intestine to form phospho-glyceric acid.

GLUCOSES.

The glucoses must be regarded as the first aldehyds of mannite, although in their chemical combinations they behave as pentatomic alcohols. They differ from the hexatomic alcohol mannite in possessing two atoms less of hydrogen, and they present the group of atoms COH, which distinguishes all aldehyds.



The glucoses may be classed as follows :—

Fermenting with yeast and reducing Barreswill's solution.	Yielding saccharic acid by oxidation	Dextro-rotatory	Glucose.
		Laevo-rotatory	Muscle sugar.
	Yielding mucic acid by oxidation . .	Inactive . . .	Chondroglucose. Cane-sugar. Mannite.
Not fermenting, and not reducing Barreswill's liquid		Dextro-rotatory .	Lactose.
			Inosite.

Glucose (dextrose).—This sugar is a normal constituent of certain tissues and fluids of the body. The blood contains, on an average, .9 per 1000 (Claude Bernard). The normal urine is said by some (Blot, Brücke) to contain small traces, but it has never been isolated, and the tests applied merely demonstrate the existence of some reducing agent without proving it to be glucose. The muscle-sugar extracted by Meissner from muscular tissue appears to be identical with glucose. It has also

been obtained from the thymus and other glands, and is present in the liquor amnii. The question of its existence in the liver shall be considered in a subsequent chapter. Normal bile contains none.

Pure glucose crystallizes in four-sided prisms, which are often agglomerated into warty lumps. They are insoluble in æther; soluble in alcohol and in water (equal parts of cold water after some time will effect complete solution). It is precipitated from solution by acetate of lead and by ammonia. The aqueous solution possesses a dextro-rotatory power of $+56^\circ$ for yellow light (when quite fresh the dextro-rotatory power is $+104^\circ$, but it gradually falls to the above constant point). One of the most characteristic properties of this substance is the readiness to undergo fermentation. Of this process there are two chief varieties:—(1) *Alcoholic*. This takes place in aqueous solutions, in presence of yeast, and most rapidly at a temperature of 25 C. (77 F.). The process results in the formation of ethyl alcohol and carbonic acid $C_6H_{12}O_6 = 2C_2H_5O + 2CO_2$. Traces of other alcohols are also found. (2) *Lactic*. This occurs in the presence of decomposing nitrogenous matter, especially of casein. It is supposed to be due to the action of a special ferment. In the first stage lactic acid is formed; it then goes on to the formation of butyric acid with evolution of hydrogen and carbonic acid.



Glucose is found in the small intestine during digestion, being derived from the amylaceous materials of the food by the action of the ferments of the saliva and pancreatic juice, and the cane-sugar is also changed into glucose. Part of the latter is immediately absorbed, and what remained in the intestine is changed into lactic and butyric acids:



Others explain the formation of butyric acid in the way given above.

Lævulose.—Under the influence of the inverting ferment the cane-sugar introduced with the food is changed into equal parts of glucose and lævulose. The latter is, accordingly, always found in the intestine during digestion.

Inosite. $C_6H_{12}O_6$.—This sugar is found in the muscles, especially in the heart (where it was first discovered by Scherer); also in the kidneys, the liver, the lungs, and spleen (Cloetta); the supra-renal capsules, brain (Müller), cord, and testicle. It is found in diabetic urine, and, according to E. Külz, is a normal constituent of that fluid. Inosite, although existing in small quantities in certain articles of our food, such as peas, beans, raisins, wine, &c., is chiefly formed within the system, but at the

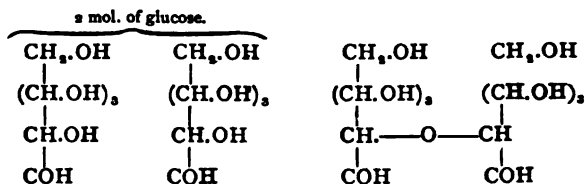
expense of what constituents of the tissues has not been shown. As its presence in the excretions, at least in quantity, is very exceptional, it must be decomposed, and is, probably, eliminated in the form of carbonic acid and water.

Pure inosite crystallizes in large rhombic efflorescent tables, soluble in water; insoluble in æther and alcohol. It has no action on polarized light, and does not reduce metallic salts in solution. It is capable of undergoing the lactic fermentation, but not the alcoholic, and, like glucose, is precipitated by acetate of lead and ammonia.

Test.—Evaporate to dryness on a piece of platinum foil, add a little ammonia and chloride of calcium, and a characteristic bright violet colour is produced.

SACCHAROSES.

The *saccharoses*, or polyglucic alcohols, are condensed glucoses; being formed by the union of two molecules of glucose, and dropping one molecule of water.



Lactose (milk-sugar) $\text{C}_{12}\text{H}_{22}\text{O}_{11}$.—This is the only saccharose found in the system and is only met with in milk. Its mode of formation is still obscure. It is not derived directly from the sugar of the ingesta, because the latter is always changed into glucose before absorption; but many think that it may be formed in the mammary gland at the expense of the glucose brought there by the circulation. After the injection of glucose into the blood of rabbits, less is eliminated in the urine during lactation than in case of other rabbits (Becker); and, after a similar experiment, glucose has been found in all the secretions, except the milk (Bernard).

When lactose is injected into the blood it rapidly disappears, being changed into glucose, and, probably, undergoes the same series of changes as the latter before elimination.

Pure lactose forms rhombic, colourless, crystalline prisms (four or eight-sided), which are insoluble in alcohol and in æther, but soluble in water. The aqueous solution possesses a dextro-rotatory power of $+\cdot 59\cdot 3^\circ$ for

yellow light. (It is greater in the freshly-made solution; $+93^{\circ}.1$). It easily undergoes the lactic fermentation, but is almost incapable of the alcoholic. Boiling with dilute mineral acids converts lactose into *galactose*; a substance which easily undergoes alcoholic fermentation.

HYDROCARBONS OF THE FORMULA $(C_6H_{10}O_5)_x$.—ANHYDRIDES OF GLUCOSSES.—The formula $C_6H_{10}O_5$ represents a certain compound (*glucosane*), obtained by heating glucose to a temperature of 170° C. (338° F.). The latter loses a molecule of water and yields glucosane and its polymeric forms, glycogen, amidon, &c.

Glucose, $C_6H_{12}O_6$; Glucosane, $C_6H_{10}O_5$; Glycogen, $(C_6H_{10}O_5)_x$; Amidon, $(C_6H_{10}O_5)_x$; Cellulose, $(C_6H_{10}O_5)_x$.

Glycogen ($C_6H_{10}O_5$)_x?—This substance is found, during adult life, in the liver (enclosed in the hepatic cells), in muscles, and in white blood corpuscles. During foetal life, it is found in most of the tissues and organs, and also in the placenta and amnion. Its physiological importance will be considered in a later chapter.

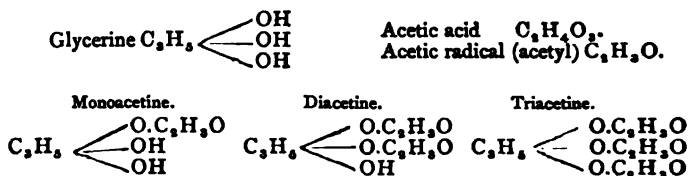
Dextrine ($C_6H_{10}O_5$)_x?—This substance has been found in the blood, especially that of herbivora, by Claude Bernard and others. It is probably derived from the food, as it has been found absent from the blood of dogs, when fed exclusively on meat. When introduced into a blood-vessel it is changed into glucose, though not very rapidly.

Phenol (*phenic acid*, *carbolic acid*) C_6H_5O .—This compound is derived from benzine, by the substitution of the hydroxyl radical HO for an atom of hydrogen. A small quantity is formed in the intestine during pancreatic digestion, and also as a result of putrefaction. Brieger has shown that human faeces always contain a certain quantity of phenol, and Landolt and Munk have found it in human urine; but it does not, as at one time believed, exist normally in human urine in the free state, but combined with sulphur, in the form of phenol-sulphuric acid, or, rather, phenol-sulphate of potassium (E. Baumann). It is probably derived from the phenol formed in the intestine, which is absorbed into the blood.

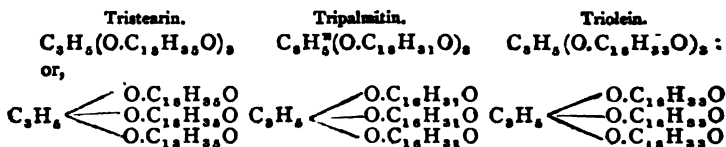
FATS.

Acids of the acetic and oleic series combine with glycerine to form the ethers or glycerides, which are popularly known as fats. The ethers are alcohols, in which the H of the hydroxyl

radical HO is replaced by an acid radical. As glycerine, a tri-atomic alcohol contains three hydroxyls, there are three varieties of corresponding ethers, according as one, two, or three of the hydroxyl radicals come to be replaced by a corresponding number of those of the supplanting acid. For example, if we take the ethereal combinations of glycerine with acetic acid we shall have :—



The fats found in the human body are stearin, olein, and palmitin, in the form of *tristearin*, *tripalmitin*, and *triolein*.



Tristearin and tripalmitin are both solid at the ordinary temperature of the body, and are held in solution by triolein, which is fluid. All the fats of the human body are formed by a mixture of these three in variable proportions, the largest being always that of palmitin.

Fats are present in all the tissues of the body and in all the fluids, except the urine. In the tissues, they are found as part of the elementary structures, or enclosed in separate cells. The latter are sometimes found to contain crystals of stearin or palmitin. In the liquids of the organism the fat is chiefly found in the form of minute droplets suspended in the fluid.

The proportion of fat in the human body is obviously very variable. Burdach gave an average estimate of five per cent. of the whole weight, Moleschott, two to five ; but it is evidently impossible to give any very accurate idea. The following table (from Gorup-Besanez) gives the mean per-centage of fats found in the principal fluids and solids of the organism.

Sweat	...	...	.001	Vitreous Humour	...	.002
Saliva	...	...	.02	Cartilage	...	1.3
Lymph	...	...	.05	Bone	...	1.4
Synovia	...	...	.06	Crystalline Lens	...	2.
Liquor Amnii	...	...	.06	Liver	...	2.4
Chyle	...	...	.2	Muscles	...	3.3
Mucus	...	...	.3	Hair	...	4.2
Blood	...	...	.4	Brain	...	8.
Milk	...	...	4.3	Adipose Tissue	...	82.7
Bile	...	...	1.4	Marrow of Bone	...	96.

The fats taken into the alimentary canal, before being absorbed, are either emulsified or saponified, as we shall see when we come to deal with the subject of digestion.

The exact nature of the metamorphosis undergone by the fats of the organism, before elimination from the system, is still involved in obscurity. A small portion is eliminated without undergoing any change—in the sebaceous matter, sweat, &c. But fat is not found in the free state in the secretions, even in cases of the most rapid emaciation, and must be eliminated in great quantity by the lungs and skin, probably in the form of carbonic acid and water. The metamorphosis of fats was formerly believed to be due to simple oxidation; but the experiments of H. Schulz are perhaps sufficient to explode this idea. He passed, for long periods together, pure oxygen gas over melted fat at the temperature of the blood, but failed to obtain carbonic acid gas till the temperature was raised to 116° C. (240° F.). It seems, then, that the destruction of fats in the system is chiefly due to a species of fermentation, analogous to, if not identical, with that produced in the alimentary canal, under the influence of the pancreatic juice; and it has been shown by Gorup-Besanez that ozone and also pure oxygen, in presence of the alkaline carbonates, effect the saponification of fats with great rapidity. A process nearly similar takes place in presence of decomposing albuminoids, as is exemplified by the formation of adipocire (a mixture of the palmitate and stearate of lime), during the putrefaction of dead bodies.

When the destruction of fats is effected by oxidation, with the final result of the formation of carbonic acid gas and water, the question arises whether any intermediate products are formed, such as formic, acetic, and butyric acids; but this result, although extremely likely, has not been conclusively proved. The presence of fat is of great importance in connection with the

maintenance of the temperature of the living body. Being a bad conductor of heat, it opposes mechanically the radiation of that produced in the interior of the body. By its decomposition it is one of the most important agents in the liberation of heat in the organism, and indeed the fat collected in the body represents a genuine store of combustible material. Its mechanical uses in padding the various prominences of the body, in rounding off its angles, forming buffers in various situations, and so protecting the different organs from external shocks—are sufficiently obvious.

SOAPS.

Small quantities of alkaline soaps are found in solution in every part of the body in which fats are met with. These are the oleates, stearates, and palmitates of sodium and of potassium, and their presence is most easily demonstrated in the chyle, lymph, blood, and bile. A portion of these fats are absorbed as such from the intestine, where they are formed by combination with the soda of the bile of the fatty acids, set free by the action of the pancreatic juice on the fatty materials of the food. But a part is also formed in the above-named fluids. For it has been found that even the emulsified fat, which is absorbed by the intestinal villi, and passes into the blood, gradually disappears, whilst the proportion of soaps increases to a corresponding degree.

The soaps are, previous to elimination, probably in turn decomposed into fatty acids, which undergo oxidation, and alkalies, which combine with the available acids to form salts.

The physiological importance of soaps is derived from their complete solubility in water, and their power of dissolving fats. The exercise of the latter function promotes of course the absorption of fats, and allows the latter to be conveyed by the various fluids to all parts of the body.

NITROGENOUS ORGANIC COMPOUNDS.

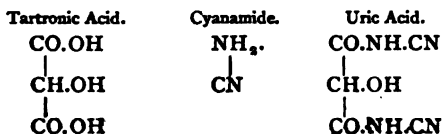
ACIDS.

Sulphocyanic Acid. CNHS.—This acid is found in combination with potassium or sodium. Its presence can be easily demonstrated in the saliva. It has also been found in the urine (Sertoli, Munck, Gschleiden), milk (Mosso), and in blood (Leared).

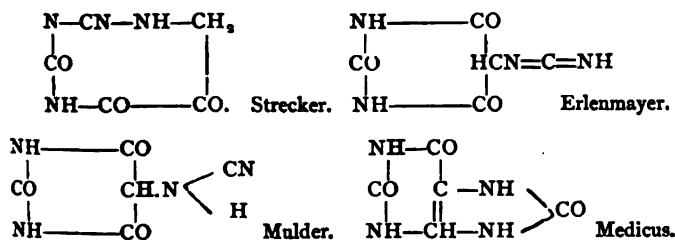
Uric Acid.—To this acid is intimately related a series of compounds, whose exact chemical composition, as well as physiological importance, still remains obscure; these are xanthin, hypoxanthin, sarcin, and guanin.

Guanin	.	$C_5H_4N_4O$.
Sarcin	.	$C_5H_4N_4O$.
Xanthin	.	$C_5H_4N_4O_2$.
Uric Acid	.	$C_5H_4N_4O_3$.

A small quantity of free uric acid is found in the urine, but the great bulk is in combination with alkalies, especially in the form of the acid urate of sodium. Traces of the alkaline urates have also been found in the blood, kidneys, spleen, lungs, liver, brain, and muscle plasma. The exact chemical constitution of uric acid is not yet settled. Boeger regards it as a tartronic-cyanamide formed by the union of a cyanamide radical with tartronic (oxymalonic) acid.



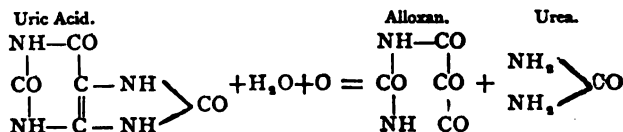
Other formulas which have been proposed for uric acid are the following :—



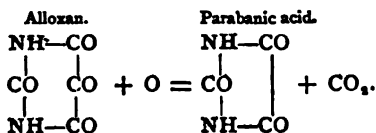
The history of uric acid is still involved in obscurity. Where it is formed, from what tissues or compounds it is derived, and what may be the nature of the intermediate substances connected with its production, are questions to which we cannot even yet

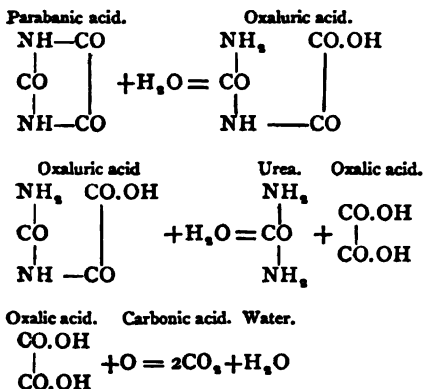
give any satisfactory reply. The resemblance of the formulæ of xanthin, sarcin, and guanin, gives probability to the idea that it comes from these substances by oxidation. Rheineck, by treating uric acid with sodium amalgam, has obtained sarcin and xanthin by reduction, but failed to obtain the converse change by any of the devices which he employed. A remarkable fact connected with the history of uric acid is, that it forms the chief product of the metamorphosis of nitrogenous matter in both birds and reptiles, two classes of animals of which one is distinguished by the rapidity, and the other by the slowness of their oxidations. In the former, urea is entirely absent from the urine, and its place is taken by uric acid, and even when urea is given to fowls it does not appear in the excretions, but the amount of uric acid of the latter is increased (H. Meyer, Jaffe). The ingestion of benzoic acid or quinine have been found to increase the amount of uric acid excreted (Meissner), while the quantity is diminished by sulphate of quinine (Ranke), by inhalation of oxygen (Eckhard, Ritter), of protoxide of nitrogen (Ritter). The use of animal food increases the amount excreted, while it is greatly diminished by an exclusively vegetable diet.

It is generally believed that a large proportion of the uric acid formed in the system is not eliminated as such, but undergoes further oxidation. It was formerly believed that urea was the resulting product, but this idea does not find general favour at present, although the artificial oxidation of uric acid undoubtedly gives rise to the formation of urea. By oxidation with acids we get—

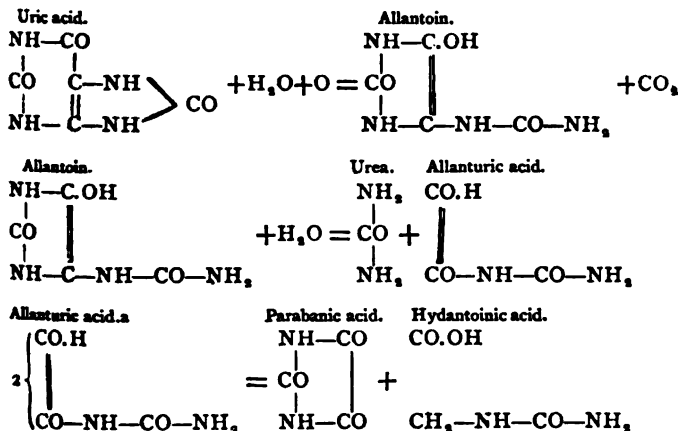


The further stages of oxidation may be represented by the following equations:—





All these products of decomposition have been found in the body excepting parabanic acid. By oxidation with alkalis uric acid yields allantoin and carbonic acid, and allantoin by hydration is converted into urea and allanturic acid, and allanturic acid in its turn becomes decomposed into parabanic and hydantoinic acids.



Parabanic acid is further changed into oxalic acid and urea,

as already seen : hydantoinic acid when treated with hydriodic acid becomes decomposed into glycocholl, carbonic acid and water. Allanturic or hydantoinic acids have not been found in the human organism, as already mentioned of parabanic acid ; allantoin, however, is found in the liquor amnii and in the urine of the foetus at birth. After giving uric acid internally to dogs, allantoin appears in the urine in considerable proportion (Salkowski).

Frerichs, Wohler, Neubauer, and Stockvis have all asserted that the ingestion of uric acid increases the urea of the renal secretion, and the results of their observations, although denied by Gallois, have been more recently confirmed by Zabelin. The theory that a portion, at least, of the urea eliminated pre-exists in the system in the form of uric acid, receives probability from the fact that many causes which derange the nutrition of the system, and retard the processes of oxidation, cause a marked increase of the amount of the latter compound discharged with the urine.

Uric acid when quite pure forms a crystalline powder, colorless, tasteless, and odorless. The crystals usually approach the elliptical or rhombic form, but vary greatly, according to the purity of the specimen examined. It is very insoluble, requiring about 15,000 parts of cold water to take it up, and refusing to be acted on by ether or alcohol. It is dissolved by the alkalies, excepting ammonia, and also by solutions of many of the alkaline salts, whilst sulphuric acid takes it up without decomposition.

Besides having recourse to the use of the microscope, the presence of uric acid may be demonstrated by certain color tests.

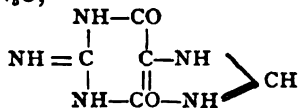
Proust's reaction (murexide test). This is done by evaporating to dryness and adding one or two drops of nitric acid. This gives a red color, which is changed to purple on the addition of ammonia.

Schiff's reaction. It is applied by adding to the fluid to be tested sodium carbonate, to ensure the solution of the uric acid, and dropping on paper moistened with a solution of a salt of silver. If uric acid be present a brown stain is formed.

Dietrich's reaction. Add a solution of hypochlorite of sodium in presence of iodine. A rose-red coloration is produced, which disappears on addition of an excess of solution of soda.

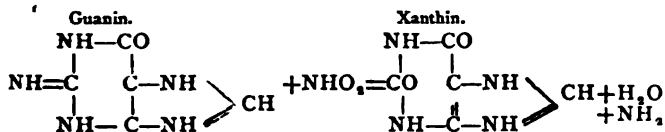
An alkaline solution of uric acid, like glucose, reduces Fehling's (or Barreswill's) solution.

Guanin, $C_5H_5N_5O$,



This compound was first obtained from guano, from which circumstance it has derived its name. Recently it has been found in small quantities in the human liver, pancreas, and some other organs; also in muscle juice. In the arachnoids it represents the last stage of proteid metamorphosis.

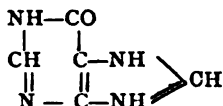
By the action of nitric acid Strecker has changed guanin into xanthin.



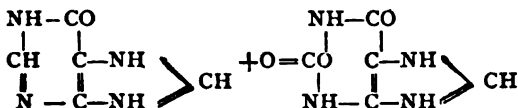
In a series of experiments on the rabbit Kerner found that the ingestion of guanin caused a marked increase in the excretion of urea. These facts would indicate that the guanin formed in the human body is further changed into xanthin and urea.

Guanin unites with acids, alkalies and salts, to form crystallisable compounds. In the pure form it is an amorphous white powder, insoluble in water, alcohol, ether and ammonia.

Sarcin (*hypoxanthin*) $\text{C}_5\text{H}_4\text{N}_4\text{O}$,

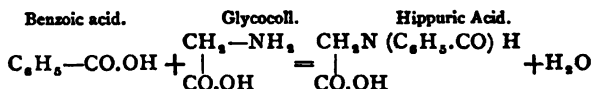


This compound is a normal constituent of many of the tissues. It is found in muscles and in the medulla of bones; in the liver, spleen, pancreas, and supra-renal capsules, and appears in the blood and urine in leukaemia. It is a product of the metamorphosis of proteids, and is changed into xanthin by the oxidising action of strong nitric acid.



Xanthin. $C_5H_4N_4O_2$.—This substance is found in many of the organs : liver, pancreas, spleen, thymus, brain, muscles, &c. Traces are found to exist in the urine as a normal constituent, and it forms a rare variety of vesical calculus, in one of which it was first discovered. It accompanies guanin in the system, and is supposed to be eliminated in the form of uric acid.

Hippuric Acid. $C_9H_9NO_3$.—This acid is a glycocoll in which an atom of H is replaced by the radical benzoyl, $C_6H_5.CO$. It abounds in the urine of herbivora, and is found in small quantity in human urine, especially during the first few days of extra-uterine life ; also, according to some authorities at least, in blood, sweat, and in the substance of the supra-renal capsules. It is formed in the body by the union of glycocoll with benzoic acid.



The use of this acid as a medicine accordingly increases the amount of hippuric acid in the urine, also the ingestion of certain vegetables, such as asparagus, prunes, whortle-berries, fruit of the arctic briar, &c. It is similarly increased after the ingestion of such things as cinnamic or quinic acids, and other kindred substances.

The hippuric acid of the urine does not exist in the free state, but in the form of hippurate of sodium, or (in case of the horse), hippurate of calcium.

Besides being derived from the ingesta, hippuric acid may originate from the decomposition of the proteids of the system. It has also been demonstrated by experiment that the kind of food which causes an increase in the quantity of this substance in the urine of one animal fails to do so in the case of another. Opinions are also at variance as to the place in which the union of the two factors, benzoic acid and glycocoll, takes place. Kühne and Hallwachs referred it to the liver, where the glycocoll was already formed, because they found that after deligation of the vena portæ benzoic acid passed unaltered into the urine ; but if benzoate and glycocholate of soda (or glycocoll) were both injected into the vessels, hippuric acid was formed. On the

other hand it was found by Bunge and Schmiedeberg that after extirpation of the liver of a frog the injection of benzoic acid and glycocholic acid into the lymph sacs of the dorsal region was followed by the appearance of hippuric acid in the renal secretion. According to Shepard and Meissner the manufacture of hippuric acid should be referred to the kidney, because none of this substance is found in the blood of herbivora, even after extirpation of the kidney; and also that after the injection of benzoic acid into the blood, hippuric acid is not found in the saliva or cutaneous secretion. Also by causing defibrinated blood, to which benzoic acid and glycocholic acid had been added, to flow through the kidney immediately after removal from the body, hippuric acid was always formed. If blood was replaced by serum in this experiment, hippuric acid failed to appear, so that the corpuscles seem to play an essential part; and this idea is borne out by the discovery of Hoffmann, that blood deprived of its oxygen by carbonic oxide also fails to form hippuric acid.

It has also been said that hippuric acid may be formed by the oxidation of other substances: from tyrosin (Hallwachs, V. Maack, Fröhde); from succinic acid (Kühne); but these conjectures have not been verified by the results of the experiments of other observers.

It is probable that the whole of this substance, which is formed in the urine, is eliminated as such, and it does not seem to have any physiological importance but as a product of excretion.

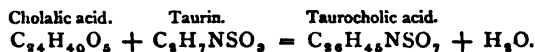
Hippuric acid is readily soluble in boiling water and in alcohol, less so in ether, and requires 600 parts of cold water to take it up. When crystallised from an aqueous solution it forms fine colorless needles, or whitish, semi-transparent four-sided prisms, according as the solution used is saturated or dilute. They have a somewhat bitter taste, but no odor. Heated to 240°C . (464°F .), hippuric acid is decomposed into hydrocyanic acid, benzoic acid, and nitro-benzol. In chemical combination it is found to be monobasic, and its salts (excepting the iron salts) are freely soluble in water.

When introduced into the alimentary canal, hippuric acid is decomposed into benzoic acid (which appears in the urine) and glycocholic acid (H. Weiske).

Reaction of Lücke.—Evaporate the fluid to be tested with an excess of nitric acid, and heat the residue; it gives an odor of bitter almonds. This reaction is common to it with benzoic acid.

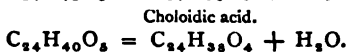
BILIARY ACIDS.

These acids are, in man, two in number: *glycocholic* (*cholic acid* of Gmelin), $C_{26}H_{48}NO_6$, and *taurocholic* (*choleic acid* of Demarquay), $C_{26}H_{46}NSO_7$. Those acids may be looked upon as derived from the union of a non-nitrogenous acid, *cholalic acid*, $C_{24}H_{40}O_6$, with a nitrogenous substance, *glycocol*, $C_2H_5NO_2$, in case of glycocholic acid; and *taurin* ($C_2H_7NSO_3$) in case of taurocholic acid. Elimination of water accompanies both combinations.



These acids exist in the bile in the form of glycocholate and taurocholate of sodium; the former predominating largely in the case of human bile; the latter alone exists in the bile of the dog and other carnivora. In the bile of salt water fishes the biliary acids are combined with potassium. The origin of these acids is still very obscure, but they are generally believed to be formed in the liver by the union of cholalic acid with glycocol and with taurin respectively. All three factors are generally supposed to be derived from the proteid constituents of the body. According to Bayer the cholalic acid of man's bile is a special acid, whose formula is $C_{18}H_{28}O_6$, and for which he suggests the name of *anthropocholic acid*.

According to Ritter and Beaunis, the glycocholates form two-thirds and the taurocholates one-third of the solids of human bile; but many other authorities reverse the proportion. In the intestine they are decomposed into their above-named respective constituents, and cholalic acid itself forms dyslysin and choloidic acid.



Hoppe-Seyler looks upon choloidic acid as merely a mixture of cholalic acid and dyslysin. The amount of these products of decomposition found in the fæces is not at all in

proportion to the quantity which passes into the intestines, and we must then admit that the great bulk finds its way back into the circulation by absorption. Their subsequent course is not definitely understood. Schiff believes that they find their way to the liver, to be again added to the biliary secretion, but this idea does not meet with general favour. He found that the injection of biliary acids under the skin, or into a blood-vessel, always increased the biliary secretion, but Huppert arrived at the opposite conclusion by an elaborate series of experiments on rabbits with biliary fistulæ. On the other hand, the experiments of Leyden and Tappeiner go to prove that the absorption of the biliary acids from the intestine is in much smaller proportion than generally believed. The idea advocated by Frerichs and Stædeler—that the acids were afterwards converted into pigment—finds hardly any advocates at the present day.

Glychocholic acid crystallises in long, fine, glistening needles; but very slightly soluble in cold water, soluble in hot water, alcohol, glycerine, acetic acid; insoluble in ether. The taste is at first saccharine, and afterwards bitter; the reaction is strongly acid. The characteristics of the sodium salt are very similar. Its aqueous solution dissolves a small quantity of neutral salts. Both the salts and the free acid possess a dextro-rotatory power over polarised light.

Taurocholic acid is less stable in composition than the preceding, and like it has a specific dextro-rotatory power, and the solubility is similar. It crystallises in fine silken needles, which are rapidly changed by contact with the air into an amorphous mass, soluble in water and alcohol, and insoluble in ether. The crystals of both acids are highly deliquescent.

Both acids, as well as cholalic acid and bile itself, give the characteristic reaction with Pettenkofer's test.

Inosic acid. $C_{10}H_{14}N_4O_{11}$.—This acid has been found in muscles only. It is probably derived from the proteids of muscle by decomposition.

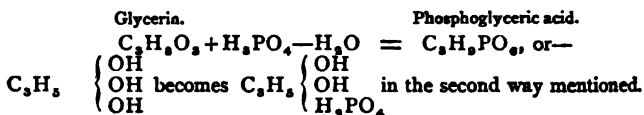
Cryptophanic acid. $C_{10}H_{14}NO_9$.—This acid has been discovered in the urine by Thudichum. According to this author it is accompanied by another acid, *paraphanic*, whose properties he has not yet studied.

BODIES ANALOGOUS TO FATS.

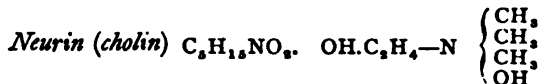
Lecithin. $C_{82}H_{144}NPO_8$.—This substance is found in considerable quantity in the substance of the brain and spinal cord, chiefly (in the form of *oleo-palmitic lecithin*) com-

bined with oleic and palmitic acids. It is also found in blood corpuscles, and in nearly all the fluids of the organism. Its source and mode of formation are still unknown.

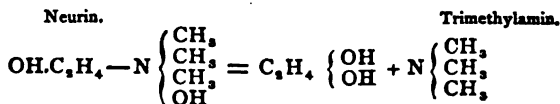
The products of decomposition of lecithin are *phosphoglyceric acid* and *neurin*. *Phosphoglyceric acid*, $C_3H_5(OH)_2PO_3H_2$, is a combination of glycerine and phosphoric acid, minus a molecule of water; or it may be described as a compound of these two, in which a hydroxyl radicle (HO) of glycerine, is replaced by a molecule of phosphoric acid H_3PO_3 , the latter losing an atom of hydrogen at the time of combination:—



This acid is easily decomposed into phosphoric acid and glycerine.

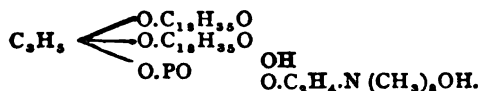


This substance is decomposed by heat into ethylic glycol and tri-methylamin.



In neurin one hydroxyl, OH, is united to ethylic glycol, the other to methylamin. Its composition explains the frequent occurrence of trimethylamin in the tissues and fluids after death. In order, then, to the formation of lecithin we must replace in the phosphoglyceric acid (1) two hydroxyls (HO) of the glyceric compound by radicals of a fatty acid (oleic, stearic, palmitic); (2) an atom of the hydrogen of the phosphoric acid by neurin—the latter, at the same time, losing one

hydroxyl radical : then with stearic acid we have the following formula :—



And similarly for the other fatty acids.

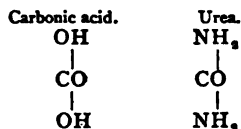
Lecithin appears to contribute to the formation of taurin, and neurin is found in the bile of some animals.

Cerebrin (*cerebric acid*, *cerebrote*), a substance apparently allied to lecithin, differs from the latter in not having any phosphorus. Its formula has not been determined.

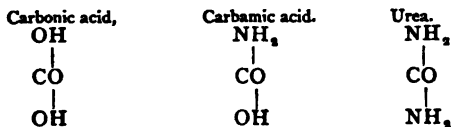
Protagon, obtained from brain tissue by Liebreich (1865), appears, from the researches of Diaconow and Hoppe-Seyler, to be a mixture of lecithin and cerebrin. Their views are, however, strongly opposed by Gamgee.

Nuclein (Miescher) has been discovered in pus corpuscles, and more recently in the brain, spermatic fluid, cells of certain tumours, &c. It appears to be a mixture of an albuminoid and a phosphorous-holding compound.

Urea. $\text{CH}_4\text{N}_2\text{O}$.—This substance is a carbamide (carbonic diamid) and may be derived from carbonic acid by replacing the two hydroxyl radicals each by the group of atoms, NH_2 :—

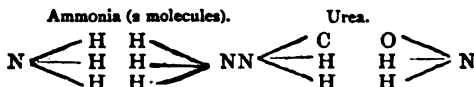


Between these two compounds there exists an intermediate, *carbamic acid*, which has not yet been isolated.



A molecule of urea may also be looked on as formed from

two molecules of ammonia in which two of the hydrogen atoms are replaced by the *carboxyl* radical CO.



In its turn urea easily forms carbonate of ammonia by the addition of water, and this is again decomposed into carbonic acid and ammonia.

This compound is metameric with cyanate of ammonium, each having the same atomic constituents. Carbamate of ammonia, when heated, yields water and urea.

Urea is one of the last stages of the metamorphosis of proteids, and there is no doubt that the great bulk of the nitrogen introduced into the system is eliminated in this form. The marked increase of this compound, after the ingestion of nitrogenous food, shows that its proportion mainly depends on this source, while its persistence in the urine during starvation proves that it is also a product of tissue-change. The experiments of Bechamp, and more recently of Ritter, have demonstrated the formation of urea by the oxidation of proteids: the re-agent used being permanganate of potash. Whether the chief source of urea be the albumen of the tissues or the albumen of the circulation still remains a matter of dispute. It was believed that the urea was entirely formed by the oxidation of uric acid, and it was affirmed by Becquerel that the quantity of the latter present was always in inverse ratio to that of the urea. This idea of the connection between the two substances has not been borne out by late observations. Creatin and creatinin have also been supposed to be among the sources of urea.

The amido-acids—leucin, sarcosin, tyrosin, and glycocoll—are supposed to be among the intermediate substances in the formation of urea from the products of proteid metamorphosis. It has been shown that the ingestion of leucin and glycocoll is followed by an increase in the urea of the renal secretion, and that the whole of the nitrogen of the leucin and of the glycocoll is represented in the urea (Schultzen and Nencki).

Urea has also been supposed to be formed at the expense of *cyanic acid*; $2(\text{CO.NH}) + \text{H}_2\text{O} = \text{CH}_4\text{N}_2\text{O} + \text{CO}_2$. There is no doubt that this acid is formed in the system, and it has also

been obtained artificially by the combustion of albuminoids in the presence of alkalis, but the exact nature of the retro-grade change is not yet definitely settled.

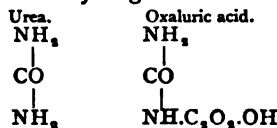
Urea has been supposed by some physiological chemists to be derived from certain ammoniacal compounds, and a considerable amount of probability is given to the hypothesis by the fact that ammonia is formed by the decomposition of albuminoid substances, and that its presence has been determined in the blood and certain excretions, while, on the other hand, the loss of two molecules of water changes carbonate of ammonia into urea. Experiments have also gone to prove that in some animals, at least, where the chloride or carbonate of ammonium has been given internally, a part of the nitrogen has been excreted with the urine in the form of urea.

Pure urea crystallises in the form of long, thin, glittering needles, or four-sided prisms with pyramidal ends, according as the solution is concentrated or dilute. They are readily soluble in water and in alcohol, insoluble in ether. Strong acids or alkalis decompose urea with production of carbonate of ammonia and carbonic acid. The same change is produced by the action of a specific ferment in an aqueous solution of urea. In presence of nitrous acid it is at once decomposed into carbonic acid and free nitrogen. It readily unites with acids and bases; the more important of the resulting compounds are the nitrate and the oxalate.

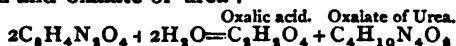
In addition to the crystals formed by evaporation, and those of the nitrate and oxalate produced by the addition of the corresponding acids, the presence of urea may be ascertained by several reactions.

Tests.—(a) Mercuric nitrate gives a precipitate which will not form when sodium chloride is present in excess. (b) On treating a solution with nitric acid containing nitrous vapors, carbonic acid and nitrogen are evolved. (c) The same gases are given off in colorless mixture when an excess of nitric acid and a small proportion of mercury is added. (d) The addition of cupric sulphate and caustic soda to an aqueous solution of the melted crystals gives a violet color.

Oxaluric Acid. $C_2H_4N_2O_6$.—This acid may be looked on as formed by the substitution of the oxalic acid radical $C_2O_2.OH$ for one of the atoms of hydrogen in urea.



Heated in presence of water this acid is decomposed into oxalic acid and oxalate of urea :—

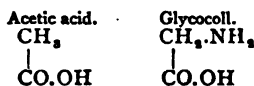


Traces of this acid have been found in the urine in the form of oxalurate of ammonia, which forms beautiful characteristic crystals. Its intimate relation with uric acid has been shown under the head of the latter substance, and it is regarded by some authorities with apparent probability as an intermediate product between uric acid and urea.

Allantoin. $C_4H_6N_2O_3$.—This substance is intimately related to uric acid and urea. It may be derived from the former by oxidation, and when treated by boiling nitric acid, or one of several other re-agents, it, in its turn, forms urea and other collateral products, allanturic acid, &c. It is found in the liquor allantoidis and in the urine of the foetus, and continues to appear during the first week of extra-uterine existence. It is also found in the urine of pregnant women, and in that of some animals,—cat, dog, &c. It is probably derived from uric acid, and having regard to the chemical facts above mentioned, would seem to be an intermediate product of retrograde metamorphosis between this acid and urea.

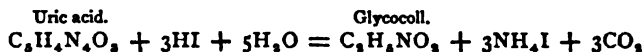
When isolated, this substance forms small, transparent, prismatic crystals. They are tasteless and inodorous: soluble in cold water (160 parts), neutral in reaction, insoluble in ether and in cold alcohol; soluble in boiling alcohol and in solutions of the alkaline carbonates.

Glycocoll (glycin) $C_2H_5NO_2$.—This substance is amido-acetic acid.

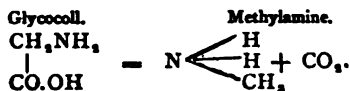


It has not been found free in the human body, but does exist as such in the muscles of the *Pecten irradians*. It enters into the composition of the glycocholic acid of bile, and must be formed in the intestine by the decomposition of the latter, still it has not been found in the intestinal contents, whether it is that it undergoes immediate decomposition, or enters into new combinations, or passes into the blood by absorption.

Glycocoll is formed when uric acid is treated with hydriodic acid at a moderately high temperature.



Under the influence of heat glycocoll is decomposed into methylamin and carbonic acid.

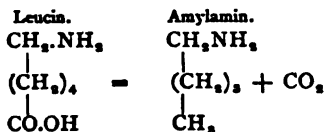


By oxidation with permanganate of ammonia glycocoll is decomposed into carbonic acid, carbamic acid, oxalic acid, oxamic acid, and water. As we have seen when dealing with urea there is reason to believe that glycocoll, at least under certain circumstances, may give rise to the formation of urea.

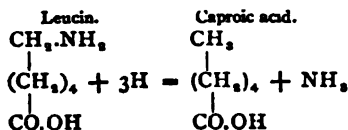
Glycocoll possesses a sweet taste and acid reaction. It forms large, hard, colorless crystals, in shape rhombohedral or quadrangular prisms, and of saccharine odor. They melt at 170°C. (338°F.); are soluble in cold water; insoluble in cold ether and cold alcohol; slightly soluble in hot alcohol. A boiling solution gives with the hydrated oxide of copper a blue solution which deposits, on cooling, needle-shaped crystals of a blue color.

Leucin. $\text{C}_6\text{H}_{13}\text{NO}_2$.—This compound is amido-caproic acid. It is found in the substance of most glands, especially in the pancreas and its secretion, and is formed during the decomposition of albuminous substances, and during the digestion of such matters with the pancreatic juice. It may also be made artificially by acting on such substances with sulphuric acid or caustic potash.

By heating, leucin is decomposed into amylamin and carbonic acid.



By the action of hydriodic acid leucin is decomposed into caproic acid and ammonia.

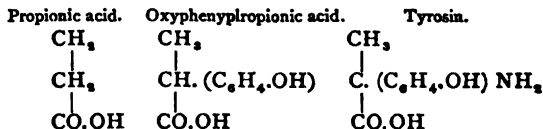


The action of sulphuric acid on leucin develops ammonia and valeric acid. With permanganate of potash it forms oxalic acid, carbonic acid, valeric acid, and ammonia. As already mentioned, leucin is probably eliminated in the form of urea.

It forms very thin, flat crystals, of a brilliant white color, tasteless and inodorous, soluble in water, and having a neutral reaction. They feel oily to the touch, and when impure, as they often are, form rounded masses of considerable size. It is insoluble in ether, slightly soluble in alcohol.

Seiger's reaction.—Evaporate a small quantity with nitric acid on platinum foil; it leaves a colorless residue which, on heating with some drops of a solution of soda, assumes a yellow, or yellowish-brown color, and at last collects to form an oily drop which rolls about on the surface of the metal.

Tyrosin. $C_9H_{11}NO_3$.—This substance is amido-oxyphenylpropionic acid. Oxyphenylpropionic acid is formed from propionic acid by the substitution of the oxyphenyl radical $C_6H_4.OH$ for one of the atoms of hydrogen, and tyrosin is in its turn formed from oxyphenylpropionic acid by dislodging an atom of H and replacing it with the radical NH_2 .



Tyrosin accompanies leucin, and has been found as a normal constituent of the spleen and the pancreas of the calf, and in the tissues of the arthropods. It probably is not a normal constituent of the human body, but has been found in pathological conditions in the blood, bile, urine, &c., especially in acute yellow atrophy of the liver.

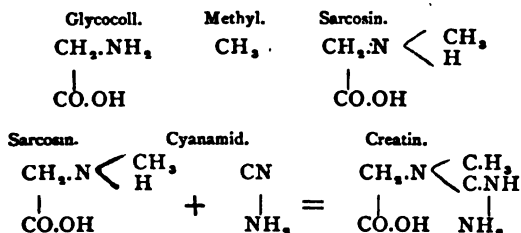
Tyrosin crystallises in feathery needles of microscopic size, colorless (snow-white in mass), tasteless and inodorous. They are slightly soluble in cold water, almost insoluble in hot water and in acid and alkaline solutions; insoluble in alcohol and ether.

Hoffman's reaction.—To a solution in a test-tube add some drops of a neutral solution of nitrate of mercury, boil for some time, and a rose color is obtained, and finally a red precipitate.

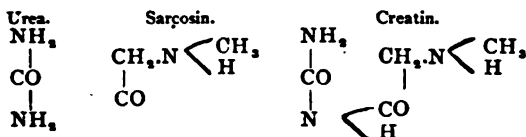
Piria's reaction.—Heat the substance in a watch-glass with some drops of concentrated sulphuric acid; when the solution is cold add a little water, and then carbonate of lime so long as effervescence continues;

filter and evaporate to a very small bulk, and add a couple of drops of a solution of chloride of iron (neutral solution). A violet color indicates the presence of tyrosin.

Creatin. $C_4H_9N_3O_2 + H_2O$.—Creatin may be said to be formed by the union of sarcosin and cyanamide. Sarcosin, again, is a methylglycocoll, or a glycocoll in which one atom of hydrogen has been replaced by the methyl radical CH_3 .



Or, creatin may be regarded as a compound formed by replacing one atom of the hydrogen of urea by an equivalent of sarcosin, minus the hydroxyl radical OH.



and, as a matter of fact, creatin is decomposed in the system, by the addition of water, into sarcosin and urea.

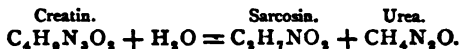
Creatin is not a normal constituent of urine, and its supposed presence in that fluid is probably due to the easy conversion of creatinin into this substance by hydration. The source of creatin is undoubtedly from the metamorphosis of albuminoids, and probably those of muscular tissue. According to Sarokow, the heart contains more creatin than other muscular tissue, and the quantity is increased by activity of the muscle, but his results have not been confirmed by later observers.

The mode of elimination of creatin is somewhat more easily understood. In great part, at least, there is every reason to believe, it is converted into creatinine. Sarokow believed that this change took place in the muscles during contraction, but

more careful analyses have shown that creatinin is not a normal constituent of muscle during either rest or activity (Nawrocki). Neither is this substance found in the blood during health. On the other hand, creatinin forms a normal constituent of the kidney (Kühne), and there is little doubt that the change takes place in this organ.



The ingestion of creatin has been found to increase the quantity of creatinin in the urine, and according to some, the amount of urea is increased under the same circumstances. Chemical experiments also seem to bear out this idea. Creatinin in presence of baryta water is decomposed into sarcosin and urea.



Subotin also obtained urea by digesting kidney tissue with creatin, and some other physiologists (Oppler, Perls, Zaleski) found that urea accumulated in the blood after ligature of the ureters, whilst no such increase was observed after extirpation of the kidney, but, in the latter case, the creatin of the muscles was found to increase in quantity. The contrary of these conclusions has been obtained by Voit and Meissner, while Grehant and Gschleiden found an increase of urea after ligature of the renal arteries or removal of the kidneys, as well as after ligature of the ureters.

Creatinin. $\text{C}_4\text{H}_7\text{N}_3\text{O}$.—This substance, although not belonging to the group of amido-acids, approaches creatin closely in chemical composition, as already seen. It is a normal constituent of urine, and although occasionally found in blood and in muscle, its presence is probably not constant.

Taurin. $\text{C}_2\text{H}_7\text{NSO}_3$.—This substance would seem to be derived from isethionic acid, by the substitution of NH_2 for the hydroxyl radical HO . A small quantity is found in the intestinal contents and in fæces. It has also been found in the urine of the ox, in the muscles and lungs of some other animals, and in the liver and spleen of some fishes. Combined with cholalic acid, it forms the taurocholic acid of bile. Its origin is still involved in obscurity.

The mode of elimination of taurin is also undecided. A certain proportion finds its way into the fæces. Of the remainder, part seems to pass into the urine, and the rest, by combining with cyanic acid, forms tauro-carbamic acid, which is also eliminated by the kidney. By the action of potash taurin is decomposed into ammonia, and the sulphate and acetate of potassium; the mucus of the gall-bladder has the same effect in presence of an alkaline liquid (Buchner).

It crystallises in colorless, regular six-sided prisms, soluble in water (especially if hot), insoluble in ether, almost insoluble in cold alcohol. Its solutions are neutral.

Cystin. $C_3H_7NSO_2$.—This substance is a rare urinary sediment. It is oftener found in the urine of the dog, and has been discovered in the kidney of the ox.

Its origin is unknown, but from its chemical composition it would seem to be derived from the metamorphosis of proteids, and its mode of formation is also very obscure. According to Dewar and Gamgee, cystin is amido-sulphopyruvic acid (pyruvic acid is derived from lactic acid by the loss of two atoms of hydrogen).

It crystallises in colorless rhombohedral or six-sided tablets, soluble in ammonia and the other alkalies, in the mineral acids, and in oxalic acid. It is insoluble in water, in alcohol, and in ether. Heated with a little soda on a silver plate, it gives a brown stain of the sulphide of silver. A solution boiled with a little acetate of lead and acetate of potash, gives a brown color due to the formation of sulphide of lead.

NITROGENOUS COMPOUNDS NOT CONTAINING OXYGEN.

Indol. C_8H_7N .—This substance is a product of the pancreatic digestion of albuminoids, and hence is found in the intestine and in fæces. It is also formed during the putrefaction of albuminoid substances, and may be obtained artificially by acting on them with a caustic alkali. It is the final product of the reduction of indigo. Its formation during pancreatic digestion is referred, by Kühne, to putrefaction, and not to the action of trypsin, as it will not be formed in presence of salicylic acid.

The characteristic odor of fæces is partly due to the pre-

sence of indol. It crystallises in colorless leaflets, soluble in water, and possessing a fæcal odor. It gives a characteristic red color with nitrous acid.

Scatol. C_8H_7N .—This substance is found in the fæces, and is produced by putrefactive changes in the small intestine (Brieger). It readily passes into the urine from the alimentary canal, and there gives, with hydrochloric acid, a characteristic violet-red color. It crystallises in lamellæ of a brilliant white color and fæcaloid odor, less soluble in water than those of indol. According to Brieger, it bears the same relation to indol that benzol does to ethylbenzol.

Pyrrol. C_4H_5N .—This substance is also found in the fæces. It is an amide which is formed during the dry distillation of albuminoids.

Trimethylamin. C_3H_9N .—This substance has been found in the urine in some pathological conditions. It is a product of decomposition of albuminoids, but nothing is known of its physiological import.

PIGMENTS.

Hamatin.—The properties of this pigment shall be discussed when we come to deal with the blood.

Bile Pigments.—

Bilirubin	$C_{18}H_{18}N_2O_6$
Biliverdin	$C_{18}H_{18}N_2O_4$
Choletelin	$C_{18}H_{18}N_2O_6$
Bilifuscin	$C_{18}H_{20}N_2O_6$
Biliprasin	$C_{18}H_{22}N_2O_6$
Hydrobilirubin	$C_{22}H_{44}N_2O_7$

All the other substances appear to be derived from *bilirubin*, which is the primary coloring matter of bile. This is the predominating coloring matter in the bile of man, and of carnivorous animals; *biliverdin*, in that of herbivora. The latter pigment has been found in the margins of the placenta of the bitch. *Choletelin*, which is a derivative of the other two, is not found in the organism, although some have asserted its identity with urobilin.

Bilifuscin and *biliprasin* do not exist in normal bile, but enter into the formation of most biliary calculi.

Hydrobilirubin is the *urobilin* of Jaffé, the *stercobilin* of Vaulair and Masius. It is found in the urine, especially in febrile conditions, in fæces, also in the placenta of dog and cat.

There can be no doubt that the original source of bilirubin is the coloring matter of the blood. In fact, the appearance of the crystals and even their chemical reactions are identical with those of *hæmatoidin*, the crystalline substance discovered by Virchow in old apoplectic clots (Jaffé, Hoppe-Seyler, Sal-kowski). We also know that the causes which determine the destruction of the red blood corpuscles (such as injection of solutions of the biliary acids, or of ammonia, or large quantities of water into the blood) are followed by the appearance of biliary pigments in the urine. It must, however, be added, that the change of hæmoglobin into bilirubin has not been effected outside the organism, and that, in reference to the alleged identity of hæmatoidin with the latter substance, it has been asserted by Preyer that the spectra are quite distinct.

In what part of the system bilirubin is formed is another question which demands attention. The most probable seat of its manufacture is in the liver. This is the only part (at least in the bodies of most animals) in which it is constantly present; it is always to be found in the hepatic cells, and the presence of the biliary acids is sufficient to account for its formation by their action on hæmoglobin. The only difficulty that remains is to account for the iron which must be set free during the formation of bile pigment. It is not sufficiently represented in the bile, nor in the hepatic veins.

On the other hand, some believe that the bilirubin is formed in the blood; that the hæmoglobin, on being set free from the corpuscles, is immediately changed into this pigment, and is merely separated from the blood by the hepatic cells. Experiments made with a view of determining this point, by injecting solutions of hæmoglobin into the blood, have yielded contradictory results in different hands.

Bilirubin forms sometimes an amorphous orange-red powder, sometimes deep-red microscopic crystals in the form of needles or tablets. It is insoluble in water, almost insoluble in alcohol and in ether, soluble in chloroform, benzene, alkalis, sulphuric

acid, &c. By the action of oxidising agents, or even by exposure to the air, it is converted into biliverdin. When an alkaline solution is treated by sodium amalgam, and hydrochloric acid is afterwards added, while access of air is prevented, it is changed into hydrobilirubin.

Biliverdin is an amorphous powder, insoluble in water, ether, and chloroform, soluble in alcohol and sulphuric acid, giving a solution of a greenish-blue color. With alkalies it gives a green color. It also is converted by sodium amalgam into hydrobilirubin. Oxidising agents change it into cholelin.

Bilifuscin and *biliprasin* are not found in bile when perfectly fresh, but are found in the bile taken from the gall-bladder some time after death, and also in biliary calculi.

Bilicyanin is a blue pigment of bile described by Heynsius and Campbell.

Urobilin (*hydrobilirubin*).—According to the recent researches of Jaffé, Disqué, &c., this substance is found but exceptionally in the human urine. But a colorless chromogen exists in normal urine, which does not affect the solar spectrum, but which by oxidation is transformed into urobilin: this is the *reduced urobilin* of Disqué. As already mentioned, it is found in febrile urine; we have also seen how it may be formed from the bile pigments. This transformation appears to take place in the intestine, and urobilin is found in the intestinal contents and in the fæces; a portion also passes into the blood, where its presence has been demonstrated by Maly with the aid of the spectrum analysis.

Hæmoglobin (or hæmatin), acted on by hydrochloric acid and zinc, yields a product which behaves in every way like the chromogen of urobilin.

Indican.—The chemical composition of this substance is not still well understood. It was formerly believed to be identical with vegetable indican, but the latter is a glucoside, which, when acted on by acids, yields indigo and indigoglucin; whilst the urinary indican yields indigo and sulphuric acid when treated in the same way, but no indigoglucin. It should then be classed among the sulpho-conjugate acids. According to Baumann and Brieger, it is an indoxyl-sulphuric acid of which the potassium salt has the formula $C_8H_6NSO_4K$.

We can pass from indol to indigo by a series of successive oxidations.

Indol	..	..	C_8H_7N
Oxindol	..	..	C_8H_7NO
Dioxindol	..	..	$C_8H_7NO_2$
Isatyde	..	..	$C_8H_5NO_3$
Isatine	..	..	$C_8H_5NO_4$
Indigo (white)	..	..	$C_{16}H_8NO_4$
„ (blue)	..	..	$C_{16}H_8NO$

When treated by concentrated acids, indican yields leucin, volatile fatty acids, and a red pigment, *urrrhodine* (Heller), *indigrubin* (Schunck), *rouge-indigo* (Beaunis). Indican is found in the urine, but is not a constant constituent, being in largest quantity after a meat diet. It is found in large proportion especially in certain pathological conditions, cancer of the liver, obstruction—especially of the large intestine, &c. In these cases the urine may become blue on putrefaction. In certain cases indican has also been found in the blood and in sweat. There is no doubt that the source of indican is the indol formed during pancreatic digestion. Hence all the causes which increase the production of indol, or prolong the stay of this substance in the alimentary canal, increase the indican of the renal secretion, as is shown by the result of a meat diet or the effect of intestinal obstruction.

Indican forms a syrupy mass of a clear brown color, soluble in water, alcohol, and ether, and having a bitter, nauseous taste. On heating it is decomposed, and gives a violet tint. An acidulated solution gives a blue color on the addition of chloride of calcium.

To ascertain its presence in urine, take a small quantity of the fluid, treat with fuming hydrochloric acid, and add two or three drops of nitric: on heating a violet-red coloration appears, and crystals of both blue and red indigo are formed.

ALBUMINOID MATTERS (PROTEIDS).

These form the principal solids of the muscular and nervous tissues and of most of the viscera. Most of the fluids also contain a certain proportion, those notably wanting being the cutaneous, lachrymal, and renal secretions. All these substances contain carbon, hydrogen, nitrogen, oxygen, and sulphur; the last element being wanting in mucin and elastin.

The following table (from Beaunis) gives the per-centages for the principal albuminoids :—

		C	H	N	O	S	Fe.
Albumin		52.7	6.9	15.4	20.9	0.8	—
		54.5	7.3	16.5	23.5	2.	—
Fibrine		52.5	7.	17.4	21.9	1.2	—
Casein (milk of human female)		52.3	7.2	14.6	25.7	?	—
Casein (milk of cow)		53.6	7.4	14.2	24.7	?	—
Syntonin		54.1	7.3	16.1	21.5	1.1	—
Peptone		51.4	6.95	17.1	—	1.1	—
Hæmoglobin		53.8	7.1	16.1	21.2	.3	.4
Amyloid substance		53.6	7.	15.5	22.5	1.3	—
Mucin		49.5	6.7	9.6	34.2	—	—
Collagenous substance		50.	6.7	18.	24.5	.5	—
Glutin		50.	6.7	18.1	24.6	.5	—
Collagenous substance (No. 2)		54.3	6.7	14.3	24.6	?	—
Chondrin		50.	6.6	14.4	29.	.6	—
Elastin		55.5	7.4	16.7	20.4	—	—
Keratin		50.	6.4	16.2	20.	.7	—

The chemical formulæ may be said to oscillate around this medium: $C_{54}H_{71}N_{14}O_{23}S_4$. The products of decomposition of albuminoids may be divided into nitrogenous and non-nitrogenous. They have been obtained by the action of the gastric and pancreatic juices, oxidation, reduction, &c.

Non-nitrogenous.

Volatile fatty acids : formic, acetic, propionic, butyric, valeric, capric.
 Benzoic acid.
 Aldehyds of these acids, especially essence of bitter almonds.
 Oxalic acid.
 Chondroglycose.
 Hydrogen.
 Sulphuric acid.

Nitrogenous.

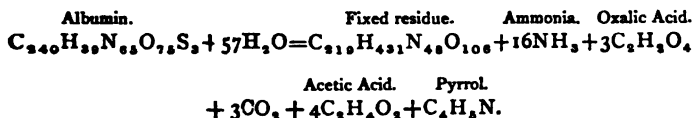
Ammonia, sulphohydrate of ammonia ; amylamin.
 Urea.
 Leucin, tyrosin, hypoxanthin, glycocoll, butalanin, alanin, tyroleucin,
 leucin, glucoprotein.
 Acids : aspartic, glutamic, glutimic, xanthoproteic, amidovaleric.
 Hydrocyanic acid.
 Indol, phenol, scattol, pyrrol.

The intimate nature and composition of the proteids is still involved in obscurity. Mulder believed that they are all formed by a combination of an organic radical protein, with the element sulphur in varying proportions. Gehrarelt also admitted the existence of a complex group of atoms, the exact nature of which he was unable to define, and forming sometimes a neutral salt (*casein*); sometimes an acid salt of soda (*albumin*).

Schutzenberger, by acting on albuminoids with baryta and heat under high pressure, obtained the following products of decomposition:—

- (1). A fixed residue.
- (2). A very small quantity of volatile products (pyrrol, indol, &c.)
- (3). Ammonia, the nitrogen of which represents about four per cent. of the weight of the albumin.
- (4). Carbonic acid.
- (5). Volatile fatty acids, especially acetic.
- (6). Oxalic acid.

This decomposition, which takes place by hydration, may be represented by the following equation:—



The fixed residue is formed by a series of amides, in which the nitrogen is more firmly combined than in the other products. These are (1) tyrosin; (2) amido-acids of the fatty series, leucin (amido-caproic acid), butalanin (amido-valeric acid), alanin (amido-propionic acid); (3) glutamic and aspartic acids; (4) glutimic acid; (5) tyroleucin; (6) leucins (combinations of tyroleucin with leucins); (7) acid aldehyds of the formula $\text{C}_m\text{H}_m\text{—NO}_2$; (8) intermediate products, gluco-proteins, which are formed when the temperature is not above 100°C . (212°F). With the exception of the last group, which are formed by hydration, all these compounds are produced by reduction.

Chemists are still at variance as to whether albumin contains any of the mineral salts. It was asserted by some authorities

that pure albumin, entirely free from salts, could be obtained by dialysis (Graham, Schmidt, &c.); but the careful researches of Hoppe-Seyler, Kühne, Alexandrowitch, and others of the highest authority, have shown that albumin always contains a small proportion of salts, even when prepared with every possible precaution.

All proteids are amorphous; their solubility in water and in acids is very variable; most are soluble in alkalies; they are all insoluble in ether, and nearly all in alcohol. The aqueous solutions are neutral. Concentrated acids or alkalies dissolve all proteids, but with decomposition, in which the various products mentioned in the above list are formed. Boiled with sulphuric acid, they yield leucin and tyrosin. They burn with an odor of burnt horn, setting free ammoniacal compounds, and leaving a residue of ash, which consists in large proportion of phosphate of lime. Left to themselves they decompose with great rapidity. Their solutions all have a laevo-rotatory action on the plane of polarised light.

Their presence can be ascertained by the following tests :—

(1) *Xantho-proteic reaction*.—Heated with concentrated nitric acid a yellow color is produced, which is changed to an orange-red on the addition of an alkali.

(2) *Millon's reaction*.—A solution of the acid nitrate of mercury gives a red color which deepens on the application of heat; and if present in quantity, the proteids are precipitated.

(3) *Reaction of Piotrowski*.—Solution of caustic potash or caustic soda, with one or two drops of a solution of capric sulphate, give a violet color, which is deepened by boiling.

(4) Make the fluid strongly acid with acetic acid, then a solution of *ferrocyanide of potassium* precipitates any proteids present.

(5) Substitute a concentrated solution of *sodium sulphate* for the ferrocyanide of potassium in the last reaction, and boil. Any proteids present are soon thrown down.

(6) *Reaction of Adamkiewicz*.—When dissolved in an excess of glacial acetic acid, every albuminate gives, on the addition of concentrated sulphuric acid, a beautiful violet color and slight fluorescence.

The following table from Gorup-Besanez gives the quantity

of albuminoids per 1000 in the principal fluids and tissues of the human body:—

Cerebro-spinal fluid	...	.9	Spinal cord	...	74.9
Aqueous humor	...	1.4	Brain	...	86.3
Liquor amnii	...	7.	Liver	...	117.4
Liquor pericardii	...	23.6	Thymus (calf)	...	122.9
Lymph	...	24.6	Egg (of fowl)	...	134.3
Pancreatic juice	...	33.3	Muscles	...	161.8
Synovia	...	39.1	Middle coat of arteries	...	273.3
Milk	...	39.4	Cartilage	...	301.
Chyle	...	40.9	Bone	...	345.
Blood	...	195.6	Crystalline lens	...	383.

The albuminoids of the organism are derived from those of the food. The essential part of the preparation for their absorption is the change into peptones. In the blood the peptones are changed into albumin, which in its turn becomes distributed throughout the tissues of the various organs of the body. It is very probable that the amount of albumin furnished by alimentation in ordinary circumstances is more than sufficient for the repair of the waste going on in the body. The excess is found in the blood as *circulating albumin*, whilst that which takes part in the formation of tissues is known as *albumin of organisation* (Beaunis).

The following are the leading characteristic properties of the proteids already catalogued:—

I. ALBUMINS.—(1) *Serum albumin*. (2) *Egg albumin*.—These substances are soluble in water, forming a neutral, transparent, yellowish fluid. From this solution they are precipitated by alcohol, mercuric chloride, nitrate of silver, and acetate of lead. Strong acids, especially nitric acid, cause coagulation. Concentrated acetic acid, or strong solution of caustic potash, change the albumen, where a large quantity is present, into a transparent jelly.

The distinguishing characters of the two varieties are: (1) Egg-albumin is coagulated by æther; serum-albumin is not. (2) Precipitated or coagulated serum-albumin is readily soluble in strong nitric acid; egg-albumin is very slightly so. (3) Strong hydrochloric acid readily precipitates serum-albumin and the precipitate is redissolved by adding an excess; the reverse holds good in case of egg-albumin. (4) The specific rotatory power of serum-albumin for yellow light is 56° , for egg-albumin is 35.5° .

II. GLOBULINS.—(1) *Vitellin*.—This is a white granular substance, insoluble in water, but very soluble in sodium chloride solutions. It coagulates at a temperature of 70° — 80° C. (158° — 176° F.) (Weyl.) By some it is supposed that vitellin is a complex substance, separable by treatment with alcohol into a coagulated proteid and lecithin.

(2) *Myosin*.—This substance when dried is very brittle, slightly transparent and elastic. It is soluble in dilute saline solutions, especially those of sodium chloride, and may be precipitated from solution, either by extreme dilution or by saturation with the sodium chloride. It is very soluble in dilute acids or alkalis. It coagulates readily by heat, and at a temperature lower than that required for the coagulation of most other proteids (55° — 60° C., 131° — 140° F.) (Kühne).

(3). *Paraglobulin* (*Fibrinoplastic substance* of Schmidt, Panum's *Serumcasein*).—Insoluble in pure water (without oxygen), but soon dissolved on shaking up with air. Soluble in very dilute alkalis without change; strong alkalis change it into alkali-albumin. Precipitated by saturation with sodium chloride (but imperfectly, according to Hammarsten). Completely precipitated by saturation with magnesium sulphate or by the passage of a stream of carbonic acid gas. The sodium chloride solutions are coagulated by a temperature of 68° — 70° C. (154.4 — 158° F.)

(4) *Fibrinogen*.—Most of the reactions of this substance agree with those of paraglobulin. Its sodium chloride solutions coagulate at a much lower temperature than those of the other: 52° — 55° C., (125.6 — 131° F.). The modes of preparation of both substances shall be described when we come to deal with the constituents of blood. Precipitated fibrinogen is a more viscid deposit, which adheres to the inside of the containing vessel, and there is no previous flocculent appearance, as in case of paraglobulin.

III. *Fibrin*.—This proteid presents a filamentous structure, the threads of which are distinguished by their elasticity. If in large quantity the reticular structure becomes less evident, so that in mass it comes to resemble pure india-rubber. It is insoluble in water and in dilute sodium chloride solutions. In dilute hydrochloric acid (1.5 per cent.) fibrin swells up and becomes transparent and jelly-like, but is not dissolved for many days, if left at the ordinary temperature. At a tempera-

ture of 40° — 60° C. (104° — 140° F.) it is dissolved in a few hours, and syntonin is formed. It is soluble in dilute alkalies, and also, although very slowly, in solutions of sulphate of sodium, nitrate of potassium, or 10 p. c. solutions of chloride of sodium. Fibrin possesses also the property of decomposing peroxide of hydrogen.

IV. PROTEINS.—(1) *Casein*.—This, when obtained pure, is an opaque, whitish and friable substance. It is soluble in dilute acids and alkalies, and re-precipitated on neutralisation. Dissolved in water, it possesses a rotatory power for yellow light of -80° .

Casein is obtained from milk by diluting with several times its bulk of water, and then adding dilute acetic acid till a precipitate begins to appear. A current of carbonic acid gas is then passed through, and the filtered precipitate is washed several times with water, alcohol and ether. Casein is also precipitated from milk when magnesium sulphate is added to saturation.

(2) *Alkali-Albumin*.—This is prepared by the action of alkalies on native albumin. It is not precipitated when its alkaline solutions are neutralised in presence of alkaline phosphates. It is with great difficulty precipitated from alkaline solution by alcohol. Its rotatory power for light varies according to the mode of preparation, which seems to show that various forms exist.

(3) *Syntonin*.—This substance is distinguished from basic albumen by the fact that it is precipitated from its solutions in dilute alkalies and alkaline carbonates by neutralisation. This takes place even in presence of the alkaline phosphates. The most characteristic of its other reactions are: (1) Its solution in lime water is partly coagulated by heat; (2) The same solution is precipitated when heated with chloride of calcium, sulphate of magnesia, or chloride of sodium.

The properties and reactions of the other albuminoids shall be described at sufficient length in connection with the tissues and fluids in which they predominate.

CHEMICAL REACTIONS IN THE LIVING ORGANISM.

The intimate nature of the chemical changes which are continually taking place in the living body, and which appear

to be essential to the manifestation of vital action, still remain shrouded in considerable obscurity. The reason is obvious when we consider that it is impossible to submit living tissue to any known process of chemical analysis without immediately destroying its vitality, and that most of our knowledge on this subject is accordingly derived from the general facts derived by the physiological chemist from examination of the substances obtained from the living body, and observation of the actions on them of the various oxidising and reducing agents. Still, so far as we can observe, the reactions of the living organism follow the general laws of chemical science, and have no special laws peculiar to vital structures. They may be conveniently grouped under three headings : analyses, syntheses, and fermentations.

I.—ANALYSES.

The analytical processes occurring in the human body, like those which are obtained in the chemical laboratory, are subdivided into oxidations, decompositions, and reductions.

a.—Oxidations.

As we have already mentioned, since the discoveries of Lavoisier, nearly all the chemical processes of the living organism were supposed to be of this nature, and life itself was supposed to be a continuous combustion—oxidations producing all the phenomena of animal life,—and it was by them that heat, motion, innervation, and all the other forms of dynamic energy were called into existence. But later researches have tended to restrict a good deal the domain of oxidation in the living body, although its great importance is still acknowledged.

The exact mechanism of these oxidations presents great difficulty. One of the hypotheses which has found most favour is that the oxygen of the blood exists there in the form of *osone*, and if this were satisfactorily proved it would make the explanation of the various chemical changes of the organic substances very much more easy. We know that the artificial oxidations, which cause the formation of products similar to those which are found in the body, require very powerful oxidising agents (nitric acid, permanganate of potash, &c.), or temperatures so elevated as to be entirely incompatible with

life. But it has been shown by Gorup-Besanez, and others, that if ozone be employed instead of oxygen, the same transformations take place at a temperature not exceeding that of the blood. This author has also shown that the presence of alkalies and alkaline carbonates facilitates the oxidation of organic substances by ozone. But the results of Gorup-Besanez and A. Schmidt on this subject have been controverted by Pflüger, Pokrowski, and others, and the presence of ozone in the blood has not been demonstrated.

That the active agent in the oxidations of the living organisms is oxygen in the nascent state is a view which has been maintained by Hoppe-Seyler. Pflüger, on the other hand, does not think either of these hypotheses necessary to explain the oxidations which take place within the body at the ordinary temperatures. At the point where the chemical change takes place the heat developed may be very considerable, but it remains localised, and is changed on the spot into mechanical movement (molecular vibrations, &c.), without at all affecting the temperature of the system at large.

Many experiments have been made with the view of determining whether the seat of oxidation is in the blood or in the tissues themselves. There is no doubt that wherever anatomical elements are found there is a continual absorption of oxygen and an elimination of carbonic acid, as was first demonstrated by the experiments of Spallanzani many years ago. Whether similar oxidising processes go on in the blood itself is not so easily determined. It has been shown that blood when left to itself becomes richer in carbonic acid; even under the mercurial air-pump arterial blood rapidly becomes dark in color, while its oxygen diminishes and carbonic acid increases. It is also found that the proportion of oxygen in arterial blood within the body diminishes as we recede from the heart. Grape-sugar injected into the femoral vein of a dog was found on examination of the arterial blood to have almost entirely disappeared. On the other hand, it has been shown by Meyer that defibrinated blood, previously deprived of carbonic acid, does not set free carbonic acid when a current of oxygen gas is passed through, and Hoppe-Seyler has demonstrated the fact that if blood be intercepted in a living artery, the outer part next the wall of the blood-vessel only becomes darkened, while the central portion retains its scarlet hue, shewing that

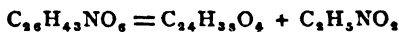
the oxygen has been utilized by the arterial wall and not by the oxidizable materials of the blood.

There can be no doubt that the greater part at least of the oxidization which takes place in the living organism has its seat in the tissues, and the experiments of Cohnheim on the "*salt-frog*" are, perhaps, the most conclusive that have been made on this point. After complete withdrawal of the blood, and filling of the blood-vessels with a dilute solution of sodium chloride, the absorption of oxygen and elimination of carbonic acid were found to go on as in the uninjured animal.

But although oxygen is largely consumed in the system, it does not follow that the processes of combination are similar to those which take place in simple combustion. We never meet with products of incomplete combustion, such as carbonic oxide, in the living organism, and the mode of production of water has not been made out. The blood leaving a contracting muscle is not richer in water than that which enters it, and the venous blood of a secreting gland is not less watery than the arterial. More striking still is the fact that where any living tissue is placed in contact with oxygen or oxygenated blood, there is no parallelism between the amount of oxygen absorbed and carbonic acid eliminated. In presence of these facts we have sufficient grounds for believing that oxidations play but a secondary part, and that the formation of substances even so simple as carbonic acid and water is due to the agency of processes much more complex than that of ordinary combustion.

b.—Decompositions.

Decomposition in its simplest form means the breaking up of an organic substance into two or more compounds, the sum of which exactly represents the original substance. The biliary acids offer a good example; glycocholic acid is decomposed into choloïdic acid and glycocoll;



and taurocholic acid is decomposed into choloïdic acid and taurin;



Dehydration is a form of decomposition. By the action of heat cholalic acid yields dyslisin and water.



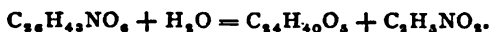
and creatin is converted into creatinin and water.



Sometimes we have a combination of dehydration and decomposition. For instance, oxalic acid at a very high temperature is broken up into carbonic acid, carbonic oxide, and water.

Disassociation is a particular form of decomposition in which the molecules of a compound become separated at a certain temperature and tension, and re-unite when the original conditions are restored: this is also called by chemists *reversible action*. The exchange of gases in the lungs and in the tissues may be looked upon as examples of disassociation (Donders).

Hydration sometimes precedes decomposition, which, in such cases, cannot take place without the addition of a molecule of water. Of this peculiar change we have an example in the formation from glycocholic acid of cholalic acid and glyccoll.



Other instances are met with in the saponification of fats, and the formation of fatty acids at the expense of fats; in the change of creatin into urea and sarcosin; of urea into carbonic acid and ammonia, &c.

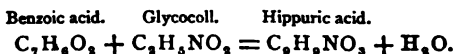
c.—Reductions.

This variety of chemical change is not of so great importance in the physiology of animal as in that of vegetable life. Plants afford a typical example of reduction in the decomposition of carbonic acid by chlorophyl, which takes place under the influence of light. In the human body examples of reduction are found in the formation of urobilin from bilirubin; of benzoic acid, at the expense of quinic acid; in the change of iodates and bromates into iodides and bromides; of indigo

blue into indigo blanc, &c. Sometimes these reductions are produced simultaneously with oxidations; for instance, malic acid introduced into the system is partly reduced, forming succinic acid, and partly oxidized, forming water and carbonic acid.

II.—SYNTHESES.

It is only of late years that this form of chemical change has been known to take place to a considerable extent in the human body. The first example was the discovery by Wöhler, in 1824, that benzoic acid, when taken into the alimentary canal, was eliminated as hippuric acid.



Also numerous other acids have been found to combine with glycocoll to form compounds analogous to hippuric acid, such as salicylic, oxybenzoic, parabenzoic, nitrobenzoic, chlorobenzoic, anisic, &c.

In some examples of syntheses the substance taken into the body, without having undergone any previous change, combines with another to form a compound more complex in its chemical structure than the original, as in the instance just given. Other examples are furnished by the union of taurin with cyanic acid to form taurocarbamic (uramidoisethionic) acid.

In another group of cases the substances introduced into the system are changed by some analytical process before undergoing the final change preparatory to elimination. In this way toluol taken into the alimentary canal is oxidised, and forms benzoic acid, which afterwards, by uniting with glycocoll, forms hippuric acid.

Besides the syntheses which follow the ingestion of certain substances, it is extremely probable that similar changes take place in the body side by side with organic decompositions.

III.—FERMENTATIONS.

Fermentations are divisible into two classes, which correspond to the two varieties of ferments, the *soluble* and the *organized*.

CHEMISTRY OF THE HUMAN BODY.

A.—*Soluble Ferments.*

The soluble ferments (*zymases* of Bechamp, *enzymes* of Kühne), such as ptyalin, pepsin, &c., are products of the secretion or of the decomposition of living cells, animal or vegetable. Their composition is excessively hard to determine on account of the difficulty of isolation, but there is little doubt that they contain nitrogen, and belong to the group of albuminoids. The best mode of separation is that of V. Willich. It consists in treating with pure glycerine the organ which contains the soluble ferment, and the latter can then be separated by one of several procedures. When dried, the soluble ferments are solid, amorphous, colorless or yellow, insipid to the taste, and soluble in water, from which they are precipitated by alcohol and acetate of lead. These ferments easily unite with albuminoids. They have also a certain affinity for substances in a state of fine division.

The following soluble ferments are present in the human body:—

1. *One changing albuminoids into peptone:*
Pepsin; gastric mucus; gastric juice; Brunner's glands; muscles; urine.
Pancreatin; pancreas; pancreatic juice.
2. *One which changes starch into sugar:*
Ptyalin; salivary glands; saliva; pancreas; pancreatic juice; liver; bile.
Gastric mucus; intestinal mucus; muscle juice; brain; kidney; urine; chyle; blood-serum.
3. *One which converts cane sugar into glucose:*
Intestinal mucus; hepatic cells.
4. *One which decomposes fats into fatty acids and glycerine:*
Pancreas and pancreatic juice.
5. *One which promotes the coagulation of the blood (fibrin-ferment);*
Liquor sanguinis.

The above table shows that the presence of soluble ferments is not limited to a single organ. The sugar-making ferment is that which is most widely distributed. Claude Bernard (1856), showed that decomposing fibrin had the power of converting starch into sugar, and the researches of Lepine have extended that property to all albuminoids and albuminoid tissues when decomposition has set in.

With regard to the formation of these ferments there are two hypotheses: according to one they are products of the secretion of certain cells, and when found elsewhere it is merely because

they have been re-absorbed. According to another, they are formed everywhere throughout the system, and are afterwards collected in special organs. But there can be no doubt that some of the ferments at least (pepsin, trypsin) are the products of the secretion of certain gland cells. This we shall see in a subsequent chapter.

B.—Organized ferments.

Latour was the first to show (1836) that the peculiar fermenting action of yeast was due to an organized structure, and not, as had been believed by Berzelius, to an amorphous substance. The most important researches in this direction have been made by Pasteur, who showed that many other forms of fermentation were due to organized substances, animal or vegetable. This variety of fermentation is accordingly brought to an end by anything which destroys or suspends the vitality of the structures to the presence of which it is due. In this way the action of organized ferments is brought to a stand-still by the action of alcohol, prussic acid, anæsthetics, &c. Compressed air and oxygen at a high tension have the same effect (Bert), but in the germinating stage they resist the action of compressed air and of alcohol (Pasteur, Feltz). Rapid movement is opposed to their action, as it has been found that bacteria do not multiply in a liquid during brisk agitation (Bert, Horvath).

Several hypotheses of the action of ferments have been offered, of which the following are the most important :—

1. *Physiological Theory*.—In 1861 Pasteur found that the butyric fermentation is due to the presence of a living organism (*vibrio*), which could exist without the presence of air or of free oxygen; that, in fact, the contact of air destroyed and stopped the fermentation, whilst it went on in presence of carbonic acid. He found that yeast behaved differently according as it was placed in contact with the air or secluded from it. In the former case it grows and forms an organized body, absorbing oxygen and giving off carbonic acid, as in the act of respiration; under these circumstances it does not act as a ferment, and does not produce alcohol. But if air is excluded alcohol commences to be formed; and similarly with other ferments, so that fermentation may be held to be "*life without*

air." Pasteur believes that all fermentations are due to the presence of these organized ferments, and moreover that all come from without, being borne by the atmospheric air.

Although many arguments have been made to disprove Pasteur's theory it is daily gaining ground, and is the one now generally accepted. It was said that eggs putrefied without the presence of any organism, but this was disproved by Gayon, who demonstrated the presence of bacteria and vibriones, and showed that when they were excluded no chemical change took place. The experiments of Cazenave and Livon show that when the bladder of an animal, with its contained urine, has been removed, after previous deligation of the urethra and ureters, the urine becomes gradually concentrated without becoming alkaline or ammoniacal fermentation taking place. The *mycoderma aceti* of vinegar, the *amylobacter* of cellulose, the *torulacea* of the ammoniacal fermentation of urine, the *vibrio* of butyric fermentation, the *vibrio* and *bacterium* of putrefaction, are specimens which show the preponderance of the influence of organized ferments.

That the various ferments, although always accompanying organized bodies, are not identical with the latter, but secreted, or in some way produced by them, is a theory advocated by Berthelot and by Hoppe-Seyler.

2. *Chemical Theories.*—One of the earliest of these is that of Berzelius, who looked upon all ferments as *catalytic* agents. But it is now known that the ferments are not invariable; for soluble ferments are gradually used up, although slowly, and organised ferments gradually increase as the process of fermentation goes on. Another is that of Liebig, who looks upon a ferment as a decomposing body, the molecular vibration of which, acting on a fermentable body of unstable composition, causes a rearrangement of its constituent atoms.

Berthelot and Hoppe-Seyler, although, as already mentioned, ascribing the production of ferments to organized bodies, regard the process of fermentation in every case as purely chemical, and believe that the ferment is gradually consumed during its action. If this could be looked upon as proved, organized ferments, in the literal sense of the term, should cease to exist. Following up this idea, Hoppe-Seyler makes the following classification of fermentations:—

I. Change of anhydrides into hydrates.

a. Ferments acting as mineral acids heated to the boiling point.

1°. Transformation of starch and glycogen into dextrin and glucose.

2°. Transformation of cane sugar into glucose and levulose.

b. Ferments acting as caustic alkalies at high temperature. Saponification.

1°. Decomposition of ethers, fats, &c., into alcohol and an acid.

2°. Decomposition of amides with admission of water; such as in the change of urea into carbonate of ammonia, that of hippuric acid into benzoic acid and glyccoll, &c.

II. Fermentation with change of oxygen into the carbon atom.

1°. Lactic fermentation.

2°. Alcoholic fermentation.

3°. Putrefaction.

4°. Butyric fermentation.

When these different forms of fermentation have been examined, we can hardly fail to be struck, as Hoppe-Seyler insists, with the striking similarity between the changes that take place in the living body and those of ordinary fermentation, especially of the putrid variety. That life is a decomposition is an assertion made by Mitscherlich, and without accepting that idea in its absolute extent, we must admit that fermentation is the process which is most characteristic of the chemistry of the living body.

A more transcendental application of this theory is that maintained by Bechamp and Estor, who not only make life a fermentation, but look upon every living organism as an agglomeration of ferments. The molecular granules which are found in the various fluids and cellular structures throughout the body are looked upon as living organisms and have received the name of *microzymas*. All the tissues of the body are, according to these authorities, formed of such minute organisms arranged in different ways, and by becoming disconnected the death of the cells is produced, and in the intestine the analogous relationship of these particles to bacteria has been studied, the latter having been seen to be formed from microzymas, and microzymas from bacteria.

CHAPTER IV.

CELLULAR PHYSIOLOGY.

THE CELL.

IN 1838, Schwann and Schleiden demonstrated that the nucleated cell in both animals and plants was the essential structural element in all the tissues, and the active agent in all the organic processes.

A Cell (according to Schwann) consists of a homogeneous membrane or cell-wall enclosing contents more or less fluid, which include a nucleus, and within this one or more nucleoli. Schwann believed that the formation of cells (*cytogenesis*) took place in a generative liquid which he called *cytoblastema* (*blastema* of Robin). In this liquid granules appeared, rudimentary nucleoli. Around each of these, new granules began to collect, and an investing membrane was formed, completing the nucleus. The nucleus then proceeded to surround itself by a layer of new granules, and as it seemed to have an active influence on the surrounding fluid, it was called the *cytoblast*. The whole was soon surrounded by a delicate membrane, forming a complete cell.

The definition given by Schwann was accepted by many eminent workers in the same department of science (Remak, Reichert, Virchow, Kölliker, Donders, &c.); but his idea of cytogenesis was completely overthrown by Remak, who, in his observations on the development of the embryo, showed that all the cells of the body were derived from the ovum. Looking upon the ovum as a true cell, of which the zona pellucida formed the investing membrane, the vitellus the contents, the germinal vesicle the nucleus, and the germinal spot the nucleolus, he found that all the cells of the embryo came from this by one of three modes of formation: (1) *fission* (*scission, segmentation*); (2) *gemmation* (*budding*); (3) *endogenous formation* (v. p. 106). By one of these methods the generation

of all new cells takes place after fertilisation of the ovum ; but, according to our conception of a cell at the present day, there is no essential difference between the three modes of formation.

Virchow has proved, in the domain of pathological anatomy, the dominance of the same law which Remak had already shown presided over the processes of physiological development, and has added his authority to the confirmation of the universal law—*omnis cellula e cellula*.

But, of later years, the idea of the structure of a cell, as defined by Schwann and adopted by Remak and Virchow, has been profoundly modified. Dujardin had remarked that in the unicellular forms of animal life (*e.g.*, *amœba*) there was no investing envelope, and the soft mass was continually changing its form, by sending out processes in different directions, so as to give rise to a peculiar form of movement. To the yielding mass Dujardin gave the name of *sarcode*, and its movements he called *sarcodic movements*. Max Schultze, following up the observations of Dujardin, found that these movements were to be seen in the cells of more complex animals, and applied to them the term *amœboid*. To the mobile mass he gave the name of *protoplasm*, a term which had been already applied by Mohl to the material of which the bulk of vegetable cells is composed.

The ease with which particles of coloring matter find their way into the interior of animal cells, and the fusion which may be occasionally seen taking place between the *amœboid* processes (*pseudopodia*) of the same or of distinct cells, disprove the necessity of the existence of a limiting cell-wall. Accordingly Max Schultze reduced the essential characters of a typical cell to "*a mass of protoplasm enclosing a nucleus*," and this definition has been adopted by Cornil and Ranvier.

Brücke has gone a step further, and finding that the nucleus is so often absent, he has come to look upon it as non-essential, and accordingly defines a cell to be a more or less homogeneous mass composed of organised substance.

Hæckel would apply the term protoplasm to the substance of nucleated corpuscles only. For the non-nucleated masses of protoplasmic matter which form the cytodes (*monera*) he has suggested the name of *plasson*.

Protoplasm (*cytoplasma*, Kölliker ; *bioplasm*, Beale ; *proto-*

zootic substance, Reichert) may be described as a semi-fluid substance, consisting of a homogeneous matrix in which are embedded large numbers of granules of varying size and appearance. These granular bodies vary in composition (fatty, amylaceous, proteid, &c.); the surrounding substance is always nitrogenous, and contains a large proportion of water (70 per cent.). Heitzmann denies the existence of isolated granules in masses of protoplasm, and describes this substance as formed by an excessively fine mesh-work of interlacing fibrils. The meshes are filled with fluid, and the pseudo-granulations are formed by the nodal points of intersection. This idea has been controverted by many authorities, especially by Langhans, who affirms that the appearance of this network is a *post-mortem* change. Hæckel believes in the existence of distinct granulations, to which he has given the name of *plastidules*. According to him they are connected to one another by excessively fine filaments, which are possessed of undulatory movements in the active state. Water is readily absorbed by protoplasm within certain limits. Particles of solid matter also find their way without difficulty into the interior of protoplasmic masses from the surrounding medium.

The vital properties of protoplasm are well exemplified in the amoeba, which is a microscopic organism found in stagnant waters. It is made up of a single mass of protoplasm. When at rest one of these bodies is of somewhat spherical form. When observed on the warm stage it is seen to be continually changing its shape. At one point of its surface a transparent elevation will be seen to form, which gradually becomes extended till it reaches a considerable length. It soon changes its shape, or becomes retracted. There are generally several of these processes (pseudopodia) protruding from different parts of the mass. In addition to the change of shape the projection of these processes gives rise to a kind of gliding movement. When the amoeba comes within a convenient distance of a foreign body which may serve for its nutrition, the latter is soon embraced by two or more of the pseudopodia, the extremities and sides of which become fused beyond it, so that it is soon surrounded completely and found to be embedded in the substance of the amoeba. Then there is an interval during which the foreign body so absorbed undergoes a process of digestion, and at the close of which the non-assimilated part is

extruded from the body of the amoeba. Cienkowsky has seen starch grains digested in this way by the amoeba.

The presence of oxygen is essential to the movements of this as of other forms of protoplasm. They are arrested by carbonic acid, by the vapour of ether, of chloroform, &c. Heat accelerates the movements, cold retards them; a very low temperature or a high one (over 40° C. or 104° F.) destroys the life of protoplasm; electricity causes retraction of its processes.

The influence of oxygen denotes the progress, in the body of the amoeba, of a function analogous to the respiration of the higher forms of animal life.

Many chemical compounds influence the movements of protoplasm unfavourably. Acids and alkalies arrest the motion. So does alcohol, opium, curara, quinine, veratrine, conia, anæsthetic vapours, &c.

Mechanical irritation causes a momentary arrest in the movement of protoplasm.

The movements are generally called forth by some external stimulus, though probably not in every case, as some maintain; some appear to be decidedly automatic.

The amoeba and other forms of protoplasmic matter are endowed with powers of reproduction which usually takes place by fusion.

From what has been said we gather that the following characteristic functional properties may be ascribed to protoplasm:—

- Irritability;
- Digestion;
- Excretion;
- Respiration;
- Reproduction.

The movements of protoplasm are of three kinds:—(1) The existence of currents in the interior, as shown by the continual motion of the granulations. (2) The amoeboid movement, already described, to which, in addition to the peculiar changes of form, the powers of absorption and progression are due. (3) Movements of displacement; of this an example is furnished by the migration of leucocytes.

The chemical composition of protoplasm is not definitely known, as the difficulties in the way of examination are extremely great, but a careful analysis has shown that the most simple protoplasm is of extremely complex chemical formation. According to Hoffmann it contains:—

- (1) Three soluble albuminoid substances; (a) an alkaline albuminate; (b) an albumin coagulable at 48° — 49° C. (118.4 — 120.2 F.); (c) an albumin identical with that of the serum of the blood.
- (2) Two insoluble albumins, one of which swells up in the form of a gelatinous mass in solutions of chloride of sodium (*hyaline substance* of Roviola);
- (3) Lecithin and cerebrin;
- (4) Soaps;
- (5) Cholesterin;
- (6) Glycogen (in lymph corpuscles);
- (7) Extractives of undetermined nature;
- (8) Inorganic salts.

STRUCTURE OF CELLS.—We have already indicated the parts of which a cell is composed; we shall now consider them more in detail, and the various properties, physical and functional, of the cell as a whole.

(1) *The Cell-wall*.—When this does not exist as a separate structure, the superficial part of the protoplasmic mass is condensed so as to form a cortical layer more resisting than the enclosed substance. When fully developed the cell-wall forms a homogeneous, amorphous, transparent membrane of variable consistence, and presenting on microscopic examination a single or double contour. It is sometimes very elastic, and easily moulds itself upon its contents; in other instances it displays a persistent rigidity. It permits the process of osmosis, or, in other words, is permeable by water and aqueous solution, but resists the passage of oils and fatty liquids.

Whether the cell-wall is in any case a separate membrane, or is in every instance merely a condensed superficial layer of the protoplasm which makes up the bulk of the cell, as it undoubtedly is in the majority of examples, is still a disputed point. Some of those who admit the existence of a separate cell-wall, believe that it may be formed by the same mechanism that determines the development of the *membranes of precipita-*

tion, obtained by Traube at the surface of contact of two colloid solutions.

An essential and characteristic difference between the cell-wall of the animal and that of the vegetable kingdom has been supposed to be that the latter is always formed of cellulose, a non-nitrogenous substance; the former being made up of a nitrogenous material. Considerable doubt has been thrown on the value of this distinction by the recent announcement (by Schutzenberger and Destrem) that the envelope of the cells of the yeast plant is made up of a complex nitrogenous substance, and not of cellulose, as previously believed. We also know that the secondary cell-membrane in the ascidia is made up of a material called *tunicine*, identical in composition with cellulose, and only differing from the latter in requiring a longer time to be changed into sugar by the action of acids.

(2) *The Cell contents*.—These are (1) the intra-cellular protoplasm, and (2) the intra-cellular juice which fills the spaces not occupied by the former. They have been already considered at sufficient length.

(3) *The Nucleus*.—This is a minute spherical body situated in the central part of the cell, more rarely near the periphery. There may be several nuclei, or the nucleus may be altogether absent, but at its origin every cell is made up of a mass of protoplasm enclosing a nucleus (Cornil and Ranvier). The nucleus is sometimes a semi-solid mass, sometimes a vesicle filled with liquid, and in its primitive state is always made up of a homogeneous mass of the protoplasm of the cell more condensed than the surrounding part. As we said in the case of the cell itself, the superficial part undergoes a process of differentiation, so that we find in its perfect state the nucleus formed by an investing membrane and the enclosed contents. The latter comprise:—

(1) A finely granular or reticular fundamental substance: *nuclear substance* of Hertwig, *nuclear essence* of Van Beneden.

(2) A nuclear liquid corresponding to the intra-cellular liquid.

(3) A minute spherule, the *nucleolus*, which may be absent ("enucleolar state" of Auerbach), or may be present in large numbers, up to a hundred or more ("multiple nucleoli" of the same author). The nucleolus, on very careful examination, presents an excessively fine reticulum analogous to that of the nucleus and of the cell itself (Heitzmann), and is enclosed by

a hyaloid membrane, which is surrounded in its turn by a layer of granules from each of which radiating filaments pass through the investing membrane into the interior of the nucleolus (Eimer). (4) Granules. Some look upon these as merely formed by the nodes of intersection of the protoplasmic reticulum already referred to. They vary a good deal in size, the larger forming the *pseudonucleoli* of Van Beneden.

The adjoining woodcut (after Klein and Noble Smith) represents the structure of a cell (colorless blood-corpuscle) with two nuclei.

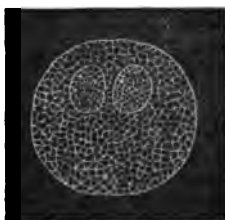


Fig. 9.

The size of animal cells varies within very wide limits. The largest cell of the human organism is the ovum, whose diameter is about $\frac{1}{16}$ of an inch. The diameter of the red blood corpuscle is about $\frac{1}{250}$ of an inch, and there are cells in the body of still smaller size. The typical form is spherical, but is very seldom retained, as it yields to the pressure of surrounding tissues, and accordingly is usually either flattened or polyhedral in form, and often assuming the cylindrical shape. The most important of the physical characters of the cell is its permeability to fluids, on account of which it is the constant seat of endosmosis and exosmosis. This causes the cell to swell out by imbibition when placed in fluids of lower specific gravity, and on the other hand determines the shrivelling and corrugation of surface which occurs when it is placed in a liquid of specific gravity higher than that of its contents.

Nutrition of the Cell.—As we have already said, the most striking peculiarities of the tissues and fluids of which the animal economy is made up are: the complexity of their chemical composition, and the instability of their structure. On account of the latter feature the contents of the cellular structures, of which, in forms variously modified, the tissues of the organism are built up, are continually breaking down (*dissimilation*), to make up for which they must be replenished from the surrounding medium by appropriating therefrom the material necessary for repair of the waste, and converting it into a part of their own substance (*assimilation*). The process of assimilation may be divided into two stages: (1) *formation* of the organic matter which is taken into the interior of the

cell ; this stage is very well marked in case of the vegetable cell, but not at all so well defined in the tissues of the animal organism ; (2) *integration* or *vivification*, by which the absorbed material becomes an integral part of the individual cell. The latter stage is equally well marked in both animal and vegetable cells.

Disassimilation takes place by oxidation either of the cell substance, or of part of the materials which had been transformed by it, but not employed for repair of the waste of its contents, and this oxidation is accompanied by the liberation of dynamic energy. The cells of the different tissues of the body have the peculiar power (so-called *elective affinity*) of selecting from the surrounding medium the materials necessary for their nutrition, and allowing only those into their interior.

Irritability.—What has been said on this subject under the head of protoplasm may be repeated of the cell. Irritability is the fundamental property of the cell, on the existence of which all the vital phenomena depend. The stimulus which calls forth the manifestation may be, as we have seen, of various kinds, mechanical, chemical, physical, or nervous. The same stimulus calls forth phenomena which may vary according to the nature of the cell. Thus the response of a muscle cell is contraction ; of a gland cell, secretion ; of a nerve cell, sensation, &c. But it may be laid down as a universal law in physiology that no manifestation of cellular activity is ever observed without the previous application of a stimulus of some kind.

From the activity possessed by individual cells, it results that each is possessed of a certain amount of vital independence in the organism, and that it is the sum of these partial existences that makes up the life of the whole.

The phenomena of cell movements may be divided into two classes : (1) *intra-cellular*, and (2) *cellular*.

(1). *Intra-cellular*.—When the cell is invested by an unyielding membrane, the movements of the protoplasmic contents do not lead to any change in the form of the cell. This has been observed in pigment cells (Lister), but more frequent examples are found in vegetable cells.

(2). *Cellular*.—properly so called, movements of the whole cell. Of this class there are four varieties :—

- (1). Amoeboid, as seen in the colorless corpuscles of the blood.
- (2). Contractile, affecting the whole cell ; exemplified in muscular fibre.

- (3). Vibratile, affecting only a part of the cell, as in ciliary motion.
- (4). Movements of locomotion, by which the cell moves as a whole, seen in the emigrant leucocytes and connective tissue corpuscles, and in spermatozoa.

Development of heat must also be a part of the phenomena of cell life, as processes of oxidation are always taking place in its interior.

Electric currents are also developed within cells.

Evolution of cells.—We have already mentioned the ideas of Schwann on the spontaneous generation of cells in a fluid furnishing the proper material. Doubts were soon thrown on this hypothesis, and before very long it came to be denied altogether, especially by Virchow. A few more recent observers have been led to believe that spontaneous development of cells may take place under very favourable circumstances, but without absolutely denying its possibility we may say that its occurrence is rare, and that the development of cell from cell is the mode of origin in the vast majority of cases. The forms of cell-multiplications usually described are: (1) endogenous formation; (2) fission; (3) gemmation.

Endogenous formation.—This takes place only in cells possessing a well-defined investing membrane. The nucleus and the protoplasm divide each into two distinct masses, the nucleus taking the lead in the segmentation. The same process then attacks each of the cells so formed, and this is repeated till an indefinite number of cells may be found within the original cell-wall, which expands to accommodate them. The latter disappears at some stage of the development, and sets the newly-formed cells free.

Recent minute examination has shown more of the changes which take place during the progress of this variety of cell-formation. The nucleus which previously presented a slightly granular or almost homogeneous appearance, becomes enlarged and elongated, and is found to be traversed by longitudinal striæ passing from one pole of the nucleus to the other. The central part of each of these striæ next becomes thickened, and the nodules so formed become continuous, forming a solid plate, bisecting the nucleus in its equatorial zone (*nuclear disc* of Strasburger). This disc is in its turn soon divided into two parts which gradually retreat from the central plane of the nucleus towards either pole, but still continue to be connected

by numbers of parallel filaments. In this stage the modified nucleus is somewhat barrel-shaped, but the outer layers of the elongated filaments which connect the terminal discs soon begin to break in the middle, and the median part becomes strangulated by degrees, till at last the division is complete, and two separate nuclei are formed.

This mode of generation is referred by some to fission or segmentation (*endogenous fission*), while they restrict the term endogenous formation to a mode of generation in which a part only of the protoplasm is employed in the formation of the new cells: this mode is also described as *free endogenous formation*.

Fission: fissiparous cell-formation.—In this mode of generation the process is similar, the only difference being that the segmentation, which in this case also begins with the nucleus, involves the cell-wall also.

Gemmation: budding.—This takes place by the development of small processes (buds) on the surface of the cell, which increase in size, and become pedunculated. The pedicle at last gives way, and sets the cell free. This mode of development is not often seen in the higher animals; it is well exemplified in the growth of the yeast-plant. In man it has been observed in the cells of the spleen.

Other special kinds of cell formation have been described: *genesis, rejuvenescence, conjugation*.

Genesis.—This is the term applied by Robin to the process which takes place when in a liquid, or between anatomical elements, either amorphous or of definite figure, where nothing exists but the plasma of a humor or blastema, certain of their immediate principles unite with one another almost suddenly, molecule to molecule, to form a solid or semi-solid substance, amorphous, or of definite shape.

Rejuvenescence.—In this variety of cell formation the entire mass of the protoplasm of one cell re-arranges itself in the formation of another, as seen in the growth of the zoospores in certain algæ (*oldogorium*).

Conjugation.—In this mode of growth, two or more protoplasmic masses belonging to different cells become fused into a single mass. It is exemplified in the formation of the zygospores of the conjugate algæ, myxomycetes, &c.

Cells, when fully formed, undergo one of two varieties of metamorphosis: (1) The cellular type is preserved, but with a

change of form ; (2) it loses its cellular character and undergoes a complete transformation. If the evolution had not been gradually traced it would be difficult, indeed, to recognise the cellular structure of the muscular fibres of the uterus during gestation ; or in the fibres of connective tissue, in a capillary blood-vessel, or in the structures of the crystalline lens. With the change of form the cell increases in size, the nucleus not so much in proportion as the other parts of its structure.

The duration of cell-life is very various. Some epithelial cells appear to have a term of existence not extending beyond a period of 12-24 hours ; those of secreting glands last a still shorter time. The duration of the cells of nails appears to be five months in summer, four months in winter (Berthold), whilst some other cells (cartilage cells, for instance) last probably as long as the life of the organism of which they form a part.

The death of cellular structures takes place in one of several different ways. It is sometimes due to *mechanical destruction*, especially in the cells of the epidermis. It very generally takes place from *chemical transformation*, as in cases of fatty or granulo-fatty degeneration, also in colloid degeneration, amyloid degeneration, calcareous infiltration, &c., &c.

The so-called cellular theory, which has found its most powerful advocate in Virchow, is based on the idea of cellular independence, first specially advocated by Goodsir, according to which the cell is the true physiological and anatomical unit. Each has its own separate existence which is, to a certain extent, independent of that of the whole organism, but the vital activity is not quite limited by its enveloping membrane. It extends beyond, and each one in this way rules a cellular territory of which it is the centre of action. The whole organism is accordingly no other than an agglomeration of cells, all of which come, by a series of successive multiplications, from a primordial cell.

But this anatomical unit was found to be much more complex in structure than had been believed. It was soon discovered that of the various parts of the cell there was one more important than the others, and on which its physiological functions seemed to depend. In this way the *protoplasmic theory* came into existence. According to this theory, protoplasm is the living substance, *par excellence* ; it is from it that all is derived, the cell comes but second in the line of importance, and there is no such marked separation between neighbouring elements. All the elements of the organism are but masses of protoplasm, more or less modified ; and, according to the views of some authorities, especially Heitzmann, the whole organism is but an immense network of protoplasm, of which the elementary structures are bound together by anastomosing processes.

Another movement has been made, of still later date, and the *plastidular theory*, to which reference has been already made under the head of proto-

plasm, has been offered as a substitute for the protoplasmic theory. This is a nearer approach to the molecular theories (such as those of Beale, of Bennett, of Bechamp, &c., according to which the anatomical and physiological units are ultimately represented by molecules endowed by special properties—*germinal matter* of Beale, *molecules* of Bennett, *microzymas* of Bechamp, &c.)

In examining the various tissues and fluids we are able to distinguish six categories of elements, each having special characteristics, both structural and functional. These are: (1) the blood cell; (2) the connective element; (3) the epithelial element; (4) the contractile element; (5) the nervous element; (6) the reproductive element—spermatozoon or ovum.

CHAPTER V.

THE BLOOD.

This fluid forms the great "internal medium" in which all the tissues of the animal organism live, and from which they derive their nutrition. By it also the waste products resulting from the metamorphosis of the various compounds throughout the body, are carried towards the excreting organs, by means of which they have to be separated and removed from the system. Its properties accordingly demand the most careful consideration, and we shall proceed to examine them under the following heads: I. Quantity; II. Physical and microscopical characters; III. Chemical composition; IV. Mode of formation of corpuscles.

I. QUANTITY OF BLOOD.

The proportion of blood in man's body has been very variously estimated. Harvey guessed it as $\frac{1}{10}$ of the weight of the body, and Haller supposed that, judging "from profuse hemorrhages, there will be 28lb. of true red blood current in the arteries and veins, of which the arteries contain only one-fifth and the veins the other four." Weber, by estimating from the quantity of fluid required to inject a dead body, calculated the amount to lie between 11 and 15lb. Valentin withdrew a quantity of blood, and determined its per-centage of solid residuum; he then injected a definite quantity of water and withdrew a second portion of blood, in which he ascertained the loss of solid constituents. In this way the weight of blood is counted as $\frac{1}{3}$ that of the body, which averaging 140lb., will leave the amount of blood at 28lb., the same which Haller assigned. If a known quantity of a harmless and easily tested salt such as ferrocyanide of potassium, be injected into a vein and then some blood drawn, the proportion of the salt in it will also afford a rough estimate (Blake). This method, as well as Valentin's, is vitiated by the rapidity with which the injected matter may be removed by skin, kidney, &c. Bernard found that about twice as much blood could be removed after a full meal before death took place, than in case of

a fasting animal. This suggests the plentiful administration of food to those who may have to lose blood in surgical operations or warfare, and its exhibition in diminished and divided quantity in plethoric diseases.

The only instances in which a fairly satisfactory calculation has been made of the quantity of blood in the human body are in cases of the bodies of decapitated criminals. In those the same method may be adopted as is done in case of the inferior animals. This is measuring directly all the blood that escapes, after opening several of the large blood-vessels; then washing out the blood-vessels carefully and preserving the washings. Lastly, mincing up the whole body, and washing out completely the coloring matter of the blood.

The quantity of blood in the washings is estimated by diluting a known quantity of blood till it presents the same tint as that of the solution to be estimated. The tints are compared either by brushing side by side on a white surface (Welcker), or by simply comparing the fluids in glass vessels with parallel sides (Hoppe-Seyler). The proportion of blood in the washings added to that which had at first escaped from the blood-vessels gives the total quantity which, estimated in this way, is about one-thirteenth of the weight of the body (one-fourteenth, Burdon-Sanderson).

There are several sources of fallacy in this method of calculation. The difficulty of procuring a clear infusion of the mixed tissues is very great. Then a small quantity of hæmoglobin exists in muscular fibre, but the error of calculation to which this gives rise is probably a minute one. Another difficulty is presented by the fact that venous blood has less colouring power than arterial, and Gschleiden has attempted to obviate this difficulty by poisoning the animal with carbonic oxide, by which all the blood is brought to an arterial color.

The proportional distribution of the blood in the various parts of the body would be, in round numbers, as follows (Ranke):—

One-fourth	in the heart, lungs, large arteries and veins.
"	" liver,
"	" skeletal muscles,
"	" other organs.

II. PHYSICAL AND MICROSCOPICAL CHARACTERS.

Blood, when taken from the vessels of the living body, is found to be a fluid, of red color (varying from a bright vermillion to

a dark red or modena tint), having a peculiar and characteristic odor, which is greatly increased on the addition of sulphuric acid (Barreuil's test). The taste is saline and nauseous, the reaction alkaline, and the specific gravity about 1.055 (Nasse—varying from 1.045 to 1.075.)

After withdrawal from the vessels the red fluid soon becomes viscid, and in a few minutes more forms a complete jelly, so that the containing vessel can be inverted without spilling. It then by degrees separates into two parts, a pale, slightly yellowish or straw-coloured fluid (*serum*), containing a semi-solid mass floating in the centre (*clot, crassamentum, cruor, insula, placenta, hepar sanguinis*).

On examining a drop of blood microscopically it is found to consist of two parts: (1) an almost colourless fluid, *liquor sanguinis* or *plasma*, containing (2) solid particles, *blood corpuscles*, floating within it. The proportional quantities of the two constituents are respectively 64: 36 (Klein). They may be separated by filtration through a filtering paper moistened with a solution of sugar (Müller), or by keeping the blood at a low temperature, so as to retard the coagulation when the corpuscles, being of higher specific gravity, fall to the bottom (Kühne). Centrifugal force has also been utilized for the purpose of separating the corpuscles from the plasma (Pribram, Gauthier). The blood is received into a narrow tube surrounded by ice to which a machine communicates a very rapid rotatory movement in a horizontal plane. A few minutes effects the separation. Two varieties of corpuscles are recognised, the *red* and the *pale* or colorless.

The red corpuscles, *hamaties* of Gruithuisen and Robin, were discovered by Swanmerdam (1658) in the frog, by Malpighi in the hedgehog, and by Leuwenhoek (1673) in human blood. The discovery received by no means a wide-spread credence, and even Magendie believed that they were merely small air bubbles that had been taken for cells. In shape they are biconcave circular discs, with rounded edges. The breadth of a corpuscle is about $\frac{1}{1000}$ or $\frac{1}{1200}$, and the thickness about $\frac{1}{2000}$ of an inch. Examined singly they are of a clear yellow color, with a tendency to a greenish tinge; it is only in large quantity that they give the well-known deep red color. They are yielding and extremely elastic in structure, so that after being stretched or compressed they regain their original shape on being left to themselves. A marked peculiarity which has never been ex-

plained, is the tendency to collect in heaps like piles of coins. The total superficies of the red blood corpuscles of an average human being is about 2,186 metres (Welcker). Their specific gravity is about 1.105. They are composed of a colorless stroma infiltrated by a colouring matter called *hæmoglobin*.

Hayem distinguishes three varieties of size of the red blood corpuscles, of which the diameters respectively are calculated at .0085, .0075, and .0065 millimeters. Of 100 red corpuscles, 75 would be of the medium size, and of the others about 12 each. The size of the corpuscles is increased by cold, oxygen, depletion, quinine, hydrocyanic acid, and alcohol, while it is diminished by heat, carbonic acid, morphia, and also during acute febrile affections (Manasséin). The red blood corpuscles are also said to be of smaller size during the first few days of their existence than afterwards. The conspicuously small corpuscles (*microcytes*) are more numerous after hæmorrhage, menstruation, acute diseases, and in pernicious progressive anaemia (Osler).

The proportion of red corpuscles in blood increases after a meal. The maximum is attained about an hour after; it is at that time 15.5—19.4 per cent. greater than before. It then diminishes gradually during fasting. The largest proportion of corpuscles is present in the venous blood of the skin, muscles, glands, and spleen; the increase being greatest in the muscles during contraction, in the glands during repose, in the spleen during digestion (Malassez).

Enumeration of the Blood Corpuscles.—(1.) *Method of Vierordt.* This is by diluting a known (small) quantity of blood with a solution of sugar; a small quantity of the mixture is passed into a capillary tube of known calibre; under the microscope the length of the column of blood is measured, and it is then dropped on to an object-glass in a solution of gum. When this is dried, the corpuscles can be counted with a micrometer divided in squares. (2.) *Method of Malassez.*—The blood is diluted with artificial serum (1-100), and then introduced into a capillary glass tube of known calibre, and the corpuscles are then counted under the microscope by the aid of a micrometer. (3.) *Method of Hayem and Næstel.*—Blood is diluted with serum, and drawn into a graduated pipette. A drop is then let fall into a cell formed by the perforation of a glass plate of $\frac{1}{4}$ th of a millimetre in thickness, and which is placed on another glass plate. It is then covered with another piece of glass and examined with the microscope. The latter is furnished with a micrometer divided into squares whose sides are $\frac{1}{4}$ th of a millimetre each; this fraction represents the depth of the cell which contains the blood. Accordingly, by multiplying the number of corpuscles within one of those squares by 125, the number in a cubic millimetre of the mixture is obtained, and on multiplying this in turn by the figure which represents the proportional dilution, the number of corpuscles in a cubic millimetre of blood is obtained.

Other instruments which have been used for the same purpose are the *globumetre* of Mantegazza, and the *citemarimo* of Ceradini. The *hamocytometer* of Gowers, which is a modification of the instrument of Hayem and Natchet. It consists of three essential parts: (1.) A delicate pipette which is graduated up to the point at which it holds 995 cubic millimetres. This is furnished with an india-rubber tube, having a glass mouthpiece to facilitate filling and emptying; (2.) a capillary tube marked to hold 5 cubic millimetres and furnished with corresponding india-rubber tubes and mouth piece; (3) a glass cell formed as in the instrument of Hayem and Natchet, but $\frac{1}{3}$ rd of a millimetre in depth, and having its bottom divided into squares of $\frac{1}{16}$ th of a millimetre. Five cms. of blood (measured by the capillary tube) are then added to 995 cms. of a standard saline solution, and when well mixed a drop is placed in the cell. It is then examined with a microscope having a magnifying power of 400 diameters, and the corpuscles of ten of the squares are counted. By multiplying the number so obtained by 10,000 the number of corpuscles in a cubic millimetre of blood is found. The average number of corpuscles per cubic millimetre is about 5,000,000 (Welcker, Vierordt). According to Sorensen 500,000 corpuscles per cubic millimetre is the lowest number which can exist during life.

The following measurements of red blood corpuscles are from Gulliver:—

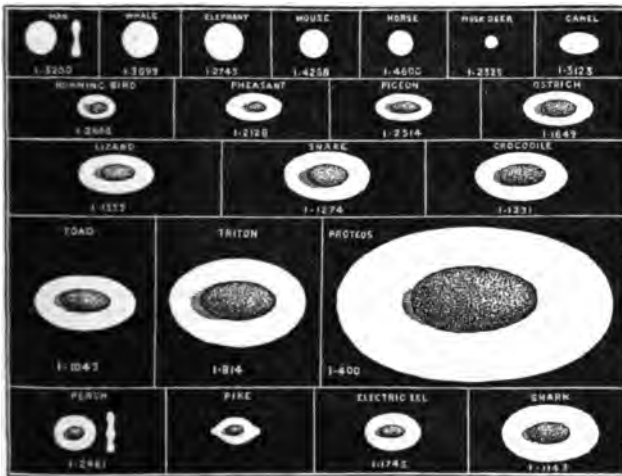


Fig. 10.

The question of the existence of a separate cell-wall in the red corpuscles has not been settled up to the present. The greater number of observers deny it altogether (Schultze, Rollett, Beale, Vintschgau, Böttcher, &c.). They base their views on direct examination, and on the action of reagents. On the other hand, some very high authorities maintain the

existence of a separate cell-wall (Reichert, Owsjannikow, Kneuttinger, Neumann), and appeal to the action of certain reagents which isolate it from its contents, such as nitric, phosphoric and other acids, alkaline solutions, alcoholic solution of sugar, &c. Preyer has satisfied himself of its existence in the cells of the salamander, and Vaillant in those of the siren. Krause, by the employment of very high magnifying powers, has convinced himself of the existence of an investing membrane presenting a double contour. Ranvier, by treating with dilute alcohol and staining with sulphate of rosaniline, has seen the peripheral layer of the corpuscles distinctly marked off from the rest as a coloured membrane presenting a double contour. The red corpuscles present the form of rounded discs in all mammals except the camel tribe, in which they are oval. They are also oval in birds, amphibians, reptiles, and in most fishes. In the lower vertebrates they are nucleated, and also in mammals during foetal life. Ranvier and Stirling have described nucleoli in the nuclei of the red corpuscles of the amphibia.

Brücke, during the action of *boracic acid* on the red corpuscles of the triton, has seen the colouring matter of the whole cell collect around the nucleus, at first forming stellate ramifications, radiating from the latter as a centre. The colouring matter all collects around the nucleus, then it passes towards the circumference, protrudes, and is at last completely separated. The coloured part (*saroid*) he looks upon as the active, living part of the cell, and the colorless portion (*akoid*) as merely forming the matrix. Krause maintains the existence of a colorless stroma, formed of radiating fibres, the mesh-work of which holds the coloring matter. Lieberkühn has observed molecular movements in the granules of the red globules, and Tarchanoff, in experiments on the corpuscles of the tadpole, has seen the granules pass from one pole to the other under the influence of electricity, and take the opposite direction when the current was reversed.

Amœboid movements have been observed in the red corpuscles during embryonic life (Schultze, Metschnikow), and have been said to be demonstrable occasionally in the adult (Winkler). They have been clearly seen in case of red corpuscles suspended in urine (Friedrich, Munk), and the dentated outline which they assume soon after removal from the blood-vessels, has been ascribed by Klebs to amœboid contraction, although this view is probably incorrect.



Fig. 11.

Fig. 11—(a) human, red corpuscle on a flat surface; (b) seen edgewise; (c) rouleaux formed during coagulation; (d) bi-concave after imbibition of water; (e) translucent appearance produced by prolonged action of water; (f) crenate outline produced by solution of gum.

Action of re-agents.—Pressure causes a wrinkling of the surface which has been used as an argument in

favor of the existence of a distinct cell-wall. The addition of *water* causes them to swell out, become globular, then discharge their colouring matter and become transparent. Solution of *chloride of sodium* causes them to become horse-chestnut shaped, and the original shape is restored by the action of carbonic acid. *Acetic acid* causes the red corpuscles of man's blood to disappear, but the outline is fairly re-defined on addition of iodine. In case of nucleated red corpuscles it makes the nucleus more clearly defined, but clears up the circumferential part of the contents. *Alkalies* cause the corpuscles to swell up, so as to assume the spherical form and finally disappear. The disappearance in case of nucleated corpuscles is preceded by a flattening of the nucleus.

The effects of the different *acids* present great varieties. We have already seen the action of boracic acid. *Tannic acid* causes the formation of a projecting knob on the surface, with a collection of the colouring matter in the centre of the cell. Concentrated *pyrogallie acid* separates the cell-substance into three parts: (1) a cortical layer; (2) a homogeneous hyaline mass (zoid of Brücke), which afterwards protrudes through the cortical layer; and (3) a yellowish-brown granular mass (Wedl). *Salts of silver* give to the outline of the corpuscles a double contour, and an elongated or angular form; after a time they break up into fragments, after losing colour. Before doing so the nuclei (in case of those of the frog), present a granular precipitate.

The vapour of *ether*, of *chloroform*, of *sulphide of carbon*, of *alcohol*, renders the blood transparent, and makes the coloring matter pass into the serum; this effect is preceded by a change in shape of the globule, which becomes irregularly spherical. *Oxygen* increases the size of the red corpuscles; *carbonic acid* diminishes it; *ozone* destroys them completely. The alternate action of oxygen and carbonic acid has been specially studied by Stricker on the globule of frog's blood. After being exposed to the vapor of warm water, carbonic acid causes the appearance of a granular precipitate within the nucleus, which Stricker believes to be paraglobulin. It disappears under the influence of oxygen. Sometimes the surface of the nucleus, and even of the corpuscle, becomes corrugated under the influence of carbonic acid, while the original form is restored by oxygen.

Bile, when added to blood, causes the red corpuscles to become pale, and then disappear quite suddenly (Kühne). *Urea*, added to defibrinated blood, causes them to assume a globular shape, and pedunculated processes form on the outside, connected to the body of the corpuscle by fine filaments (Kölliker).

The action of heat has been studied by M. Schultze up to 52° C. (125° F.). Beyond this temperature the corpuscles begin to present elevations, then bud-like processes, arranged in a variety of forms.

Electricity caused the cells to assume a dentate outline, the processes becoming elevated till they assume the appearance of needles, then these prickly elevations disappear, and the corpuscle assumes its original spherical form, and finally the coloring matter passes into the serum, leaving the corpuscle transparent.

When the stroma has been deprived of the coloring matter by electricity, refrigeration, &c., the remaining mass (*globulin*

of Denis) is found to have become lighter, and does not fall to the bottom of the vessel as before. The proportion of stroma to hæmoglobin is 1 : 13. Its chemical composition is not definitely known. The following matters have been found : (1) albuminoids, an alkali-albuminate, and globulin ; (2) lecithin ; (3) cholesterin ; (4) fats ; (5) water ; (6) alkaline phosphates (probably derived from lecithin), and alkaline chlorides (at least in those of the dog and ox). Traces of manganese have also been found. The nucleus of nucleated red globules also contains nuclein. Red corpuscles also contain a substance of unknown composition which decomposes carbonates. At a temperature of 60° C (140° F.), the stroma dissolves completely.

Hæmoglobin (*hæmatoglobulin*, *cruorin*, *hæmatocrystallin*). This substance may be separated by breaking up the red corpuscles in any of the ways already mentioned (by electricity, by addition of chloroform, ether, or bile salts, or, better still, by alternately freezing and thawing, then diminishing the alkalinity by addition of a little dilute acetic acid, treating with one-fourth the bulk of alcohol, and setting aside at a temperature of 0° C (32° F.), for one or two days. Gschleiden prepares crystals of hæmoglobin by exposing defibrinated blood to the air for twenty-four hours, then introducing it into fine glass tubes, and hermetically sealing the ends ; the tubes are kept for several days in a stove at a temperature of 37° C. (98°·6 F.), at the end of which time the blood is received in a watch glass ; when evaporation commences crystals of hæmoglobin begin to fall down. It contains 42 per cent. of iron, and Preyer has given the formula $C_{200}H_{200}N_{72}FS_4O_{172}$. The same authority gives the following classification according to facility of crystallisation :

Very difficult,	calf, pig, pigeon, frog.
Difficult,	man, ape, rabbit, sheep.
Easy, ..	cat, dog, mouse, horse.
Very easy,	rat, guinea-pig.

The crystals obtained from man's blood are four-sided prisms or rhombohedral tablets. Those of the guinea-pig are hexagonal ; all the others are rhombohedral in shape. All are of a bright blood-red colour, transparent, and doubly refracting. They are soluble in water, and the solutions are feebly acid. The solubility is in inverse ratio of their facility of crystallisa-

tion. The solutions coagulate, and albumen is separated at a temperature of 64° — 68° C. (147° .2— 158° .4 F.). The solutions are not diffusible. Hæmoglobin is decomposed by alkalis, alkaline salts, glycerine, biliary acids, urine, solution of urea, &c. It decomposes peroxide of hydrogen, and powerfully ozonises oxygen. If a drop of solution of hæmoglobin be placed on bibulous paper previously moistened with a solution of tincture of guaiacum, the red spot is surrounded by a blue ring (Van Deen's test). Hæmoglobin is decomposed by volatile fatty acids, and also by tartaric and citric acids; the iron separates as an oxide, and coloring matters containing no iron are formed.

The chemical composition varies a little in different animals. The following table gives the proportional per-centage of its elements :—

C	53.85	—	54.15.
H	7.18	—	7.32.
O	21.24	—	21.84.
N	16.17	—	16.22.
S	0.39	—	.83.
F	.42	—	.43.

Hæmoglobin exists in two forms in the blood. These are known as *oxyhæmoglobin* and *reduced hæmoglobin*. One of the greatest, and practically the most important by far, of the properties of hæmoglobin is its power of taking up a certain definite proportion of oxygen, which it easily yields up again in presence of substances which absorb this gas. When united with this loosely-combined oxygen it is known as oxyhæmoglobin; without it, reduced hæmoglobin. In some animals it is only the oxyhæmoglobin which has been obtained in the crystalline form. Oxyhæmoglobin abounds in arterial blood; reduced hæmoglobin in venous blood, but each kind of blood contains the second variety.

How the hæmoglobin is combined with the corpuscle has not been clearly made out. The fact that this substance is freely soluble in serum would seem to show that it must be retained with a certain force, whether it be chemical combination, affinity, impermeability of the superficial layer of the cell-substance, &c. Under certain conditions the crystals of hæmoglobin have been seen within the corpuscles. Reduced hæmoglobin takes up per gramme 1.52 cubic centimetres of

oxygen. Carbonic acid reduces hæmoglobin ; so does hydrogen, nitrogen, sulphide of ammonium, &c. The action of heat has the same effect, also the influence of a vacuum. Reduced hæmoglobin resists putrefaction, and also resists pancreatic digestion.

Carbonic oxide displaces oxygen from its combination with hæmoglobin and takes its place in corresponding volume. The carbonic oxide hæmoglobin has the same crystalline form as oxyhæmoglobin, and its color is the same ; it is more stable than the other, and is not influenced by reducing agents. Hæmoglobin also combines with nitric oxide, acetylene, hydrocyanic acid, sulphuretted hydrogen, &c.

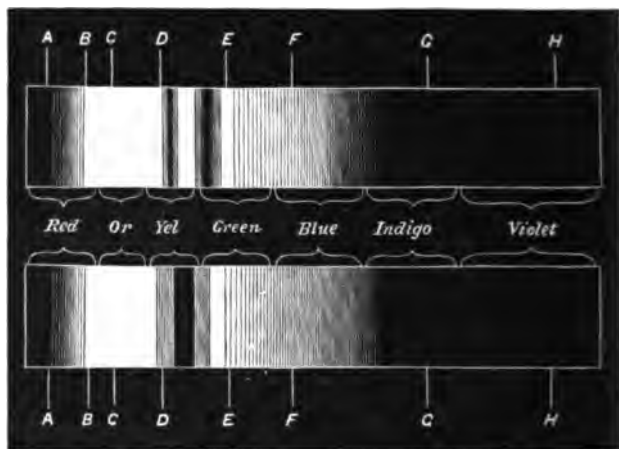


Fig. 12.

The spectroscopic appearances of oxyhæmoglobin are characteristic. Two absorption bands are present between the D and E lines, of which the one next the D line is the narrower but more sharply defined, and the only one visible when the solution is extremely dilute. Each band is darkest in the middle and fades gradually towards the margins. A portion of the red end of the spectrum is also absorbed, and a larger portion of the blue. Reduced hæmoglobin, on the other hand, gives but a single band (*reduction band* of Stokes), broad, with ill-defined edges, and situated opposite the interval between the two bands

of oxyhæmoglobin. Both spectra are represented in the adjoining wood-cut, the upper being that of oxyhæmoglobin, the lower that of the reduced.

Various products of decomposition have been obtained from hæmoglobin according to the re-agents employed. It is decomposed by acids and alkalis into (a) acid albumin, (b) an alkali albuminate, and (c) *hæmatin*. Dried in a vacuum it is broken up into *globin* and *methæmoglobin*. The following coloring matters have been derived from hæmoglobin :—

Methæmoglobin		
Hæmatin (oxyhæmatin) ...	...	$C_{88}H_{70}N_8F_8O_{10}$
Hæmochromogen (reduced hæmatin)		$C_{88}H_{70}N_8F_8O_8$
Hæmatoporphyrin ...	...	$C_{88}H_{74}N_8O_{12}$
Hæmatolin ...	...	$C_{88}H_{78}N_8O_7$
Hæmatöidin ...	...	$C_{88}H_{80}N_8O_6$

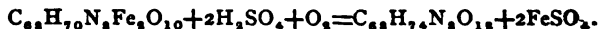
Methæmoglobin.—The chemical composition of this substance is not accurately known. Hoppe-Seyler has obtained it by deoxidising hæmoglobin by means of palladium charged with hydrogen. Other observers think that it contains more oxygen than hæmoglobin, and look upon it as a mixture of hæmatin and soluble albuminoids. It does not form crystals.

Hæmatin.—This is a reddish brown powder possessing a metallic lustre, insoluble in water, alcohol, and chloroform; soluble in alkaline solutions and in acidulated alcohol. It does not crystallise. Acted on by strong sulphuric acid it yields hæmatoporphyrin and hæmatolin (Hoppe-Seyler). It combines with hydrochloric acid to form *hæmin*, which crystallises in rhombohedral plates of a reddish-brown color (Teichmann's crystals). They are insoluble in water, scarcely soluble in warm alcohol and in ether, soluble in liquor potassæ. Their chemical composition is represented by the formula $C_{88}H_{72}N_8F_8O_8Cl_2$ (Hoppe-Seyler). An alkaline solution of hæmatin gives a broad absorption band between the C and D lines, and a great part of the blue end of the spectrum is absorbed. The solutions are dichroïc, and in thick layers appear reddish-brown to transmitted light, and olive green in a thin layer.

Hæmochromogen (reduced hæmatin).—The alkaline solutions of hæmatin are capable of being reduced by de-oxidising agents, and the reduced solution will, like hæmoglobin, again take up oxygen (one molecule for two of hæmatin) on being brought into contact with air. The spectrum of reduced hæmatin

presents two absorption bands to the blue side of the single band of the unreduced hæmatin, while the blue end undergoes less absorption. One of the bands is between D and E, the second and paler between E and F. In acid solutions it loses its iron and forms *hæmatoporphyrin*. By the action of sulphuric acid, when air is excluded, another non-ferrous compound, *hæmatolin*, is formed.

Hæmatoporphyrin (Hoppe-Seyler), *iron-free hæmatin*.—The researches of Hoppe-Seyler have demonstrated that hæmatin when acted on by sulphuric acid in the presence of oxygen forms hæmatoporphyrin and ferrous sulphate :—



The spectrum of hæmatoporphyrin presents two absorption-bands ; one between the lines C and D, the other between D and E.

Hæmatoin (Preyer), *acid hæmatin* (Stokes). This is obtained by acting on a strong solution of hæmoglobin with acetic acid, and afterwards adding ether, which carries with it all the coloring matter to the top, where it forms a dark-red layer, giving a well-marked and characteristic spectrum.

Hæmatöidin.—This is found, as we have already seen, in old blood clots, and its crystals appear to be identical with those of bilirubin.

The products of decomposition of the coloring matter of the blood are found to be as follows :—(1) An albuminoid material of which the characters vary according to the mode of decomposition ; (2) coloring matters containing iron ; (3) non-ferruginous coloring matter ; (4) oxide of iron ; (5) traces of volatile fatty acids, with formic and butyric acids ; (6) leucin and tyrosin (obtained by decomposition of hæmatin) ; (7) pyrrol (obtained by dry distillation of hæmatin).

The physiological function of hæmoglobin is to take up the oxygen introduced by respiration and convey it along the blood-vessels to the capillaries, through whose walls it finds its way to the various tissues. Of the mode of its formation in the system nobody has as yet been able to offer a plausible explanation. The only facts which seem to throw any light on this obscure point are the following :—When oxyhæmoglobin is decomposed by the action of acetic acid, yielding the hæmatoin of Preyer (a colouring matter containing no iron), and that the solution

is afterwards saturated by an alkali, the iron recombines with it to form hæmoglobin. Also, when hæmoglobin is treated by alkalies or strong acids it is decomposed into albumin and hæmatin, and when these two compounds are agitated together in presence of oxygen, they re-unite to form hæmoglobin. But the experiment of endeavoring to form hæmoglobin by synthesis of hæmatin and albumin (acid or alkaline), although often tried, has not succeeded up to the present.

WHITE CORPUSCLES.

The *white* (*pale, colorless*) corpuscles, or *leucocytes* (Robin), were discovered in 1770 by Hewson. They are somewhat spherical in form, a little larger than the red-blood corpuscles, and much less numerous, the proportion to the latter being about 1 : 500. The proportion is largely increased after eating, if fluid be taken with the meal, otherwise it is diminished (Klein). It is greatly diminished by long fasting. On account of the great rapidity with which they are broken down soon after the blood is removed from the vessels, it has been supposed that the number actually enumerated never represents with any degree of accuracy the proportion which really exists in the circulation.

The proportion of white corpuscles is increased after depletion, during lactation, local suppuration, leukæmia, quinine, turpentine, camphor, essence of fennel and of cinnamon; it is diminished by mercury, curara, essence of peppermint, and, according to some (Binz and Martin), by quinine.

A pale corpuscle is formed of a granular mass of protoplasm having no investing membrane, and enclosing from 1—5 nuclei, which are made clear by the action of acetic acid. The granular appearance is due to the presence of a meshwork of very fine fibrils (Heitzmann). But there are some which contain distinct granules in the meshes, and these are known as "*granular corpuscles*." Semmer has described corpuscles which contain red granules, "*red granular corpuscles*," which he and A. Schmidt look upon as intermediate forms between granular, pale corpuscles and colored ones.

The granular corpuscles are fewer than the ordinary pale ones and their movements are more active.

Schültze has distinguished four varieties of pale blood corpuscles:—(1) The smallest—of about $\frac{1}{3000}$ of an inch in diameter, furnished with a very large nucleus, and not present-

ing amoeboid movements; (2) of the size of red blood corpuscles, are finely granular, and send out short pointed processes in different directions, but beyond this can hardly be said to show amoeboid movements; (3) are larger than the preceding, of irregular and changing outline, enclosing fine granules, and presenting typical amoeboid movements; (4) resemble the preceding, except in the particular of presenting larger granules.

The amoeboid movements of the white corpuscles are best marked at about the ordinary temperature of the body; at 40° C. (104° F.) they cease, and the corpuscles assume a spherical form (heat tetanus); at 90° C. (122° F.) they become fusiform in shape and lose their power of recovery. Electricity also causes retraction of the processes and assumption of the spherical shape; if the discharge be sufficiently strong it destroys them.

The plasma of most mammals contains a variable number of colorless, bright, angular granules of minute size (Max Schultze).

COAGULATION.

Blood which, as it flows from the vessels of the living body, is perfectly fluid, becomes viscid in a very few (two or three) minutes, and soon after (five to ten minutes) forms a thick jelly, so that the containing vessel can be inverted without spilling. Soon drops of a clear or slightly yellowish liquid are found to collect on the surface and around the sides and at the bottom, leaving a semi-solid mass, the *clot* (*crassamentum*) floating in the centre. The latter goes on contracting in size for about twenty hours. The clot on examination is found to be made up of a substance called fibrin, which forms an excessively fine meshwork of interlacing fibrils, and containing the corpuscles in its interstices. The red corpuscles being heavier than the pale fall down sooner, and on this account the lower part of the clot is more deeply colored than the upper. The upper layer is sometimes formed by the fibrin and white corpuscles only, so as to present a yellowish (buff) color. In such specimens the upper surface presents a well-marked central depression, and from both these characteristics received the name of "*buffed* and *cupped* coat," by which it was formerly known. It was also known as the *crusta phlogistica* from the fact

that it is generally seen in inflammatory blood, on account of the greater slowness of the process in this condition giving time for the corpuscles to sink. The time occupied by the process of coagulation varies a good deal. It is slower in case of man's blood than in that of woman, and venous blood requires a longer time than arterial. Blood drawn from the capillaries does not coagulate. Menstrual blood does not clot, probably on account of the admixture of vaginal mucus, for when it escapes in large quantities it coagulates like ordinary blood. The blood of the hepatic veins also makes but a very feeble attempt at clotting.

That the presence of the corpuscles is not essential to the process of coagulation is shown by the fact that plasma—obtained free from corpuscles by allowing blood to stand at a low temperature, so as to give time for the latter to fall to the bottom—clots, when the temperature is raised a little, as firmly as if the corpuscles had not been present.

The process of coagulation is influenced by many agencies :—

It is hastened by—	Retarded by—
Rest ;	Rapid motion ;
Contact with foreign bodies ;	Smooth surfaces ;
Contact with oxygen ;	Seclusion from oxygen ; addition of
Moderate temperature ;	carbonic acid ;
Water, added in moderate quantity	Low temperature ;
(less than twice the bulk).	Water, added in large quantity ;
	Alkalies ;
	Some salts (carbonate of sodium, of
	potassium, sulphate of sodium, of
	magnesium ; alkaline chlorides ;
	bicarbonate of soda ; nitrate of potash).

To explain the intimate nature of the phenomena of coagulation numerous theories have been offered. The following are the more important :—

Theory of Richardson.—According to this hypothesis, which has been abandoned by its author, fibrin is present in the circulating blood, but is held in solution by ammonia. The latter escapes when the blood is taken from the vessels, with the immediate result of the coagulation of the fibrin.

Theory of Lister.—Lister, by many experiments performed with great care, believes that he has disproved the theory that blood within the vessels has any tendency to coagulate ; the formation of fibrin being determined by contact with foreign matter.

Theory of Lussana.—This author endeavoured to prove that fibrin was a product of the retrograde metamorphosis of the tissues, especially muscular.

The fibrinogenous substance so generated coagulated under the influence of an albuminoid compound, *globulin*, which in its turn was furnished by the destruction of the blood corpuscles (both red and pale). He asserts that the blood of a muscle after prolonged tetanisation yields half as much fibrin again as a corresponding muscle left in repose. The result of this experiment has been contradicted by Mantegazza.

Theory of Mantegazza.—According to this theory fibrin is entirely derived from the white corpuscles: its production he looks upon as a vital (not cadaveric) phenomenon brought about by irritation of the corpuscles by contact with foreign bodies, which leads to the formation of a fibrinoplastic substance, which, becoming organized, forms fibrin.

Theory of Eichwald.—Eichwald maintains that fibrin pre-exists in the blood in the soluble form. After the escape of blood from the vessels the carbonic acid of the air and that which is formed at the expense of the red corpuscles combine with the bases which had previously kept the fibrin in solution, and the latter is precipitated.

Theory of Heynsius.—He endeavors to prove that the red corpuscles take an active part in coagulation. He has shown that the quantity of fibrin obtained from plasma is much smaller than that obtained from the same bulk of blood. He has also shown by careful experiment that the addition of blood-serum to corpuscles (from which the plasma has been completely separated by exposure to a low temperature and subsequent washing with a weak sodium chloride solution), is followed by the formation of a clot almost equal in bulk to that yielded by a corresponding amount of blood.

Theory of Brücke.—According to Brücke, the fibrinogenous substance pre-exists in the blood in the form of albumin. When the blood escapes from the vessels an acid is formed which precipitates the latter. (In the last edition of his "Physiologie," Brücke inclines more to the theory of Schmidt, mentioned below.)

Theory of Mathieu and Urbain.—According to this theory fibrin exists in the circulating blood in a state of solution. After withdrawal from the vessels, the carbonic acid escaping from the red corpuscles combines to form a fibrin-carbonate, which is insoluble. He believes that alkaline salts prevent coagulation simply by combining with the carbonic acid. He also points out that if blood be taken from the renal vein and deprived of its fibrin by whipping, the addition of carbonic acid is followed by coagulation. There is no doubt that blood contains less carbonic acid after coagulation than before, and carbonic acid is set free from coagulated fibrin by the action of acids.

Theory of Schmidt.—This theory, which is the one most generally received at present, is that coagulation, or the formation of fibrin, is due to the union of two albuminous substances, *fibrinogen*, and *fibrinoplastic substance* (paraglobulin), a union which is brought about by the intervention of a third factor, to which Schmidt has given the name of *fibrin-ferment*. We shall again return to the examination of this theory.

If blood plasma (obtained free from corpuscles after delaying the coagulation by cold or addition of a neutral salt), be saturated with a neutral salt, a whitish, glutinous precipitate, of somewhat flaky appearance, is thrown down. This sub-

stance, first discovered and described by Denis, was named by him *plasmin*. That its presence is essential to coagulation is shown by the fact that, after it is removed from the plasma by filtration, the remaining fluid has lost all power of clotting, while a solution of the plasmin itself in water readily coagulates.

A further step in the investigation of the nature of coagulation was taken by Dr. A. Buchanan, who, observing that the union of two non-coagulable fluids—blood-serum and hydrocele fluid—was followed by the formation of a clot, was led to the conclusion that fibrin was formed by the combination of two distinct substances. Further study of the subject, especially in the hands of Professor A. Schmidt, has led to the isolation of the active constituents. If blood-serum be treated with solid sodium chloride or magnesium sulphate, or if a stream of carbonic acid gas be passed through, a precipitate is obtained, nearly similar in appearance to plasmin. After removal of this precipitate, by filtration and dissolving in water, the solution is found to have the power of producing coagulation of hydrocele fluid, while the serum from which it has been removed has no such effect. A similar treatment of hydrocele fluid gives a precipitate like that obtained from serum, but more flaky and less granular. This substance, after removal by filtration and diffusion in water, causes coagulation when added to blood-serum; whereas the fluid from which it has been removed is found to have lost this power. To the latter precipitate Schmidt has given the name of *fibrinogen*, while he distinguishes the former by the name of *fibrinoplastic substance*, or *paraglobulin*. There can be no doubt that the formation of fibrin is due to the union of these two substances. It would also seem that the plasmin of Denis is a mixture of both, but it cannot be conclusively asserted, as plasmin has not been separated into fibrinoplastin and fibrinogen.

The investigations of Schmidt have led him to the conclusion that the presence of a third factor is essential to the formation of a clot. To this he has given the name of *fibrin-ferment*. The following facts favour the hypothesis of its existence:—

(1.) If fibrinogen and fibrinoplastin are obtained by precipitation with a neutral salt, coagulation follows when they are mixed together: this does not occur when they are separated by the action of carbonic acid gas.

(2.) If plasma be diluted with water (eight parts of the latter

to three of the former), and one part of sulphate of magnesium be added, the mixture shows little or no tendency to coagulate. But coagulation immediately follows the addition of fibrinoplastin. This fact, when we remember that fibrinoplastin is already present in excess, seems to show that a *tertium quid* is added with the latter.

(3.) If from blood-serum the proteids are precipitated by the addition of a large excess of alcohol, and an aqueous extract be made of the precipitate, the addition of the latter to the diluted plasma above described hastens coagulation.

(4.) If liquor pericardii be removed immediately after death it is found to be spontaneously coagulable. This property is lost some hours after death ; but the addition of fibrinoplastin (precipitated from blood-serum by addition of a neutral salt) soon brings about coagulation.

The results of the experiments that have been made on the subject, go to prove that this third factor influences the rapidity of the coagulation, but not the quantity of fibrin formed. The whole of the fibrinogen is consumed in the process of coagulation ; but this is not true of the fibrinoplastin, of which an excess always remains in the serum after coagulation. Fibrinogen exists pre-formed in the living blood. Fibrinoplastin and the fibrin-ferment are formed from the products of destruction of the white blood corpuscles. According to Hayem the first step in the coagulation of blood is the decomposition of a number of hæmatoblasts, from which the threads of fibrin immediately seem to spring. Schmidt has shown that the presence of a neutral salt is also necessary : without it no fibrin is formed, even although all these factors are brought together.

The fibrin factors have been prepared by the following methods :—

(1) *Paraglobulin. Schmidt's process.*—Blood-serum is diluted with fifteen times its bulk of water, a few drops of dilute acetic acid is then added, and a stream of carbonic acid is passed through. The precipitate, which at first is a mere cloudiness, soon becomes flocculent, and, finally, granular in appearance. It is removed by filtration, and washed with distilled water till quite free from chlorides and albumen (as shown by testing with nitrate of silver and with ferrocyanide of potassium. Obtained in this way it is always impure, from the presence of traces of fibrinogen, fibrin-ferment, lecithin, &c. *Hammarsten's process.*—Blood-serum is saturated with sodium chloride in fine powder ; the precipitate of paraglobulin, which falls, is redissolved in a weak solution of the same salt, and again thrown down by addition of the salt in substance ; this proceeding is repeated several times. He also uses sulphate of magnesia as the precipitating agent, by adding to

the serum five times its quantity of a saturated solution of magnesium sulphate.

(2) *Fibrinogen. Schmidt's process.*—Hydrocele fluid, or liquor pericardii, is diluted with water, then exactly neutralized, after which a stream of carbonic acid gas is passed through for a considerable time. *Hammarsten's process.*—To a quantity of horse's blood a quarter of the bulk of a saturated solution of magnesium sulphate is added; the fluid is then filtered, and a saturated solution of sodium chloride is added to the filtered plasma. The precipitate obtained in this way is pressed between folds of filtering paper, then dissolved in distilled water and re-precipitated by sodium chloride; this process is repeated several times. In this way fibrinogen is obtained pure and free from paraglobulin.

(3) *Fibrin ferment. Schmidt's process.*—To blood-serum is added fifteen or twenty times its bulk of alcohol, and the mixture is allowed to stand for at least fourteen days, and at a moderate temperature. It is then filtered, and the precipitate is dried over sulphuric acid, after which it is rubbed up with distilled water for ten minutes, and a current of carbonic acid gas is passed through the liquid till there is no further precipitate. The filtered liquid will be found to contain the ferment. *Hammarsten's process.*—Paraglobulin is first precipitated from the serum by the magnesium sulphate method; afterwards it is diluted with a large quantity of distilled water, and treated with an alkali; a precipitate of magnesium hydrate is carried down, and with it the ferment. The precipitate is then dissolved in water, with the addition of a little dilute acetic acid, and the ferment thrown down by alcohol (or the magnesia may be removed by dialysis).

Why the blood does not coagulate within the living body is another question whose solution has given much trouble to physiologists. The theory of Brücke is, that some inhibitory influence is maintained by the healthy coats of the living blood-vessels, so as effectually to prevent the union of the fibrin-factors. The fact that the blood maintains its fluidity for a considerable period after death, when allowed to remain within the vessels, but rapidly coagulates if removed, is in favor of this hypothesis, which is further strengthened by observing that it retains its fluidity for a much longer time in the smaller veins, where it is exposed to a relatively larger proportion of vascular surface. If a piece of a large vein be included between two ligatures, then removed, and suspended by one end, the blood remains fluid for a considerable period (up to 48 hours), allowing the corpuscles to fall to the bottom, and leave the plasma on the top. Even when the upper part of the tube is removed, and the surface exposed to the air, coagulation seems to be very little hastened (Turner, Lister).

On the other hand, if a foreign body (wire thread, &c.), be introduced into a living blood-vessel, fibrin is almost immediately

deposited ; and clots invariably form when the internal coat of an artery has been injured by a ligature, or altered by disease. If the coats of a vein be crushed between strong forceps at several points of its length, coagulation will be found to take place at the injured parts, while the fluidity of the blood in the intermediate portions of the vessel is retained (Lister). Lister and Brücke have, however, arrived at contradictory conclusions on the subject, the former believing the blood is always ready to coagulate, and is only prevented from doing so by contact with the walls of the living blood-vessels, while the latter is of opinion that circulating blood has no tendency to clot, but that the contact with foreign matter is the exciting cause of the change.

III. CHEMICAL COMPOSITION OF BLOOD.

The following table (from Schmidt) gives an analysis of the blood of a man of 25 years (per 1000 parts.)

Blood (total).				Plasma.	Corpuscles.
Water	..	...	788.71	901.51	681.63
Solids	..	..	211.29	98.49	318.37
Albuminoids and extractives			192.10	81.92	296.07
Fibrin	...	..	3.93	8.06	—
Hæmatin	..	..	7.38	—	15.02
Salts	..	..	7.88	8.51	7.28
Chloride of sodium	..		2.701	5.546	—
„ potassium	..		2.062	.359	3.679
Sulphate of potassium	..		.205	.281	.132
Phosphate of sodium	..		.457	.271	.633
„ potassium			1.202	—	2.343
„ calcium	..		.193	.298	.094
„ magnesium			.137	.218	.06
Soda	..	..	.921	1.532	.341

The analysis shows the relative richness of the corpuscles in potassium salts and phosphates, and the preponderance of sodium salts, especially the chloride, which characterises the inorganic constituents of the plasma. The arrangement of bases and acids in such a table cannot, however, be taken as a true representation of what exists in the circulating blood. Many of the sulphates and phosphates are produced by oxidation of the sulphur and phosphorus of some of the proteids.

Also, carbonates are absent from the analysis, although undoubtedly existing in normal plasma.

The following table gives the result of several analyses of moist corpuscles (per 1,000 parts):—

	I. Dog (Hohlbeck).	II. Fig (Bunge).	III. Horse (Bunge).	IV. Ox (Bunge).
Water . . .	569.3	632.1	608.9	599.9
Solids . . .	430.7	367.9		400.1
Hæmoglobin . . .		261.		280.5
Albuminoids . . .	412.51	86.1		107.3
Cholesterin . . .	1.26			
Lecithin . . .	7.47	12.	391.1	7.5
Extractives . . .	2.97			
Organic salts . . .	6.49	8.9		4.8
K ₂ O . . .	—	5.543	4.92	.747
MgO . . .	—	.158	?	.017
Cl . . .	—	1.504	1.93	1.635
P ₂ O ₅ . . .	—	2.067	?	.793
Na ₂ O . . .	—	—	—	2.093

The solids of the corpuscles are nearly all made up of organic matter, the inorganic salts being less than 1 per cent. Hæmoglobin makes up the great bulk of the organic matter. In the white corpuscles are found albumin (alkaline), and a proteid closely resembling myosin. Lecithin, glycogen, and extractives are also present, and a peculiar proteid, soluble in hydrochloric acid. The estimate is made, not from white corpuscles themselves, but from pus-corpuscles, the similarity of whose composition may be inferred from their physical resemblance (Miescher).

The percentage of solids in the serum of blood is, according to Hammarsten, as follows:—

	Solids. (total.)	Albuminoids (total.)	Paraglobulin.	Serum-albu- min.	Lecithin, fats, Salts, &c.
Horse . . .	8.597	7.257	4.565	2.677	1.34
Ox . . .	8.965	7.499	4.169	3.33	1.466
Man . . .	9.207	7.62	3.103	4.516	1.588
Rabbit . . .	7.525	6.225	1.788	4.436	1.299

The proportion of inorganic salts (per 1000) in the serum of blood is given in the following table from Hoppe-Seyler. The

analysis of the blood of the dog and calf are by Sertoli, the others by Hoppe-Seyler himself.

	Man.	Dog.	Calf.	Snake.
K_2SO_4 . . .	—	—	0.414	—
Na_2SO_4 . . .	0.44	0.325	.244	1.239
$NaCl$. . .	4.92	5.915	5.390	8.485
Na_2HPO_4 . . .	.15	.072	.05	1.236
Na_2CO_3 . . .	.21	.303	1.992	2.545
$Ca_3(PO_4)_2$ }	.73	?	?	1.731
$Mg_3(PO_4)_2$ }		?	?	.923

And the proportion of salts in the ash of blood (per 100) is given in the following table. II. is the mean of four analyses by Jarisch; III. is by Verdeil; IV. by Henneberg; V. by Weber; VI. is the mean of two analyses by Verdeil; I. and VII. are by Hoppe-Seyler.

	I. Dog.	II. Man.	III. Man.	IV. Man.	V. Calf.	VI. Sheep.	VII. Chicken
Potash . . .	3.96	26.55	12.71	11.39	7.00	6.61	18.41
Soda . . .	43.4	24.11	34.9	36.24	56.65	41.92	30.00
Lime . . .	1.29	.9	1.68	1.88	.73	1.10	1.08
Magnesia . . .	.65	.53	.99	1.28	.24	.56	.22
Oxide of iron . . .	8.68	8.16	8.07	8.8	7.03	8.93	3.89
Chlorine . . .	32.47	30.74	37.63	34.23	27.3	12.67	24.14
Sulphuric acid (SO_3) . . .	4.13	7.11	1.7	1.16	1.66	1.78	1.19
Phosphoric acid (P_2O_5) . . .	12.74	8.82	9.37	11.26	4.17	5.10	26.62
Carbonic acid . . .	—	—	—	.96	—	—	—
Silicic acid . . .	—	—	—	—	1.11	—	—

To determine the proportion of hæmoglobin in blood various methods have been employed. Hoppe-Seyler dissolves a certain quantity of crystallised hæmoglobin in water, and placing the solution in a glass vessel with parallel rectangular sides, he compares the tint with that of a quantity of blood, which must be diluted till the hues are identical. The calculation is then a simple rule-of-three problem. Welcker prefers to compare the stains left by the fluids on a white surface. Preyer estimates the strength of solution of hæmoglobin by comparison of the spectra. Mantegazza examines the various solutions containing blood or hæmoglobin in a horizontal tube with glass ends, and of which the extremities can be approximated by a mechanism similar to that of an opera-glass. He examines the flame of a candle through the sanguineous solution, and interposes pieces of blue glass between the eye and the latter till the flame ceases to be visible. In this way he determines by gradation the various tints, comparing them with solutions of hæmoglobin of known strength. Worm-Muller, instead of diluting, as is done by Hoppe-Seyler and Preyer, takes a quantity of distilled water, and adds to it as much blood as is necessary to give the same tint as a given solution. To give it

an absolute value it may be compared with a solution of crystallised hæmoglobin of known strength. Hayem compares the tints given by blood diluted with varying quantities of water, till it contains a certain number of corpuscles per cubic millimetre. Malassez compares dilute solutions of blood with solutions of hæmoglobin or of picro-carminate of ammonia of known strength. The sanguineous solution is placed in a *melangeur Potain*, the reservoir of which is made with parallel glass sides; the colored fluid is placed in a glass-vessel of prismatic form, which can be moved conveniently by a rack, so as to place before the eye the layer of fluid, more or less deep, as required. The two solutions are compared through corresponding holes in a screen; a needle points out on a graduated scale the position of the prism when the tints of the solutions are identical, and the instrument is accompanied by a table which gives the proportions of hæmoglobin for each degree of the scale, these having been already estimated by experiment.

The percentage of hæmoglobin in blood has been estimated as follows:—

Man.	Woman.	
12.09—15.07	11.57—13.69	Becquerel and Rodier.
—	14.1 —14.4	Quinke.
12.5	10.7	Quinquaud.

To ascertain the quantity of urea one of the following methods may be adopted:—*Meissner's*: A quantity of blood is diluted with four times its weight of water, acidulated with dilute sulphuric acid, and the albuminoids then precipitated by heat. The liquid is then filtered and evaporated to half, when baryta water is added to precipitate the sulphates and the phosphates; the excess of baryta is then neutralized by sulphuric acid, after which the liquid is evaporated to a small quantity, and treated with absolute alcohol. The residue of the alcoholic extract is diffused in water, the liquid is rendered alkaline by carbonate of sodium, and precipitated by mercuric nitrate. The precipitate is washed and placed in water, a current of sulphuretted hydrogen is passed through to precipitate the mercury; the liquid is then evaporated to a syrupy consistence, and treated by concentrated nitric acid, which throws down crystals of nitrate of urea. *Picard's*: Blood is treated by adding an equal weight of crystals of sulphate of soda, and then boiled and filtered. The filtered liquid is treated with fuming nitric acid, and the carbonic acid liberated is fixed by the addition of carbonate of baryta, and measured by decomposition of the carbonate of baryta formed.

Gases of the Blood.—One of three different methods may be employed to separate the contained gases from the blood.
(a) *Exposure to heat.* This method, employed for the first time by Davy, and modified by Bert, is very imperfect, as it does not separate the gases completely, and is now employed only as an adjunct to other methods. (b) *Displacement.* Priestley

displaced the oxygen by hydrogen, and demonstrated its presence by its action on nitric oxide gas. Vauquelin displaced carbonic acid gas by a current of hydrogen, and his method was employed by Magnus and Bertuch, but gives, as Preyer has shown, very imperfect results. Claude Bernard utilises for the displacement of oxygen that peculiar property of carbonic oxide of displacing oxygen from its combination with hæmoglobin. (*c*) *Disengagement in a vacuum.* Mayow (1670) was the first to observe that blood yielded gas when exposed to a vacuum. Any one of three different methods may be employed for the separation : (1) the pneumatic machine, (2) boiling of water. (3) the mercurial air pump.

The following are the proportions of gas contained in : hundred volumes of blood (at 0°C and 760 mm. of pressure) :—

		Arterial blood.	Venous blood.
O	...	18	8
CO ₂	...	38	48
N	...	2	2
		—	—
Total	...	58	58

Oxygen.—Oxygen is found in the blood almost entirely combined with the hæmoglobin (forming oxy-hæmoglobin), a very small quantity being found in the plasma in a state of simple solution. One gramme of the latter substance is able to fix 1.52 cc. of oxygen (Hüfner). The connection is now known to be a form of loose chemical combination, and the hæmoglobin is always ready to give up this oxygen in presence of reducing agents, or by the action of heat, of a vacuum, or a current of another gas. The assertion that this oxygen exists in the state of ozone during its combination has not been proved. The red corpuscles are, however, capable of transferring ozone from another ozone-bearing substance to an oxidisable material. If ozonised turpentine be added to freshly-made tincture of guaiacum no change of color is produced ; but if some drops of blood be added, and the mixture agitated, a blue coloration appears, because the ozone is carried over to the tincture of guaiacum.

The proportion of oxygen in arterial blood increases with the number of red corpuscles, the frequency and depth of the respirations, wakefulness, muscular exertion, elevation of the

internal temperature, depression of the external temperature, calibre of the containing artery (because in the large arteries the density and proportion of red corpuscles are greater). The proportion diminishes after depletion, drink, during digestion, sleep, anæsthesia (except in the stage of excitement, when it is found to be increased), by lowering of the internal temperature of the body, and elevation of the external; also by inanition, pain, and even by a uniform diet. Animals of small bulk have blood less highly oxygenated; so have the very young and the very old. During asphyxia the proportion of oxygen rapidly diminishes, and has been found to fall as low as 1.5 per cent.

The proportion of oxygen in venous blood varies more than that of the arterial, and it may be completely absent in asphyxia. A considerable quantity is found in the red venous blood coming from a secreting gland, and the proportion is small in the venous blood of a contracting muscle.

Carbonic Acid.—This gas is found both in the plasma and in the red corpuscles. In the plasma it is chemically combined, and probably in three different states: (1) carbonate of soda; (2) bicarbonate of soda; (3) phospho-carbonate of soda (*Fernel's salt*). A small quantity also seems to be united in the serum to some proteid compound, probably paraglobulin. All the carbonic acid of blood is given off in a vacuum, as Pflüger has shewn; but this result is due to the fact that in the process an acid is formed which is able to decompose the carbonate of soda (Preyer, Schöffner, Afonaszew). The formation of an acid is not necessary for the separation of the part of the carbonic acid gas combined in the form of bicarbonate and phospho-carbonate, as this is easily eliminated in a vacuum.

The red corpuscles also contain a certain proportion of carbonic acid (A. Schmidt, Zuntz, Fredericq, &c.), perhaps about a tenth of the total quantity contained in blood (Setschenow). It seems to be combined with the hæmoglobin.

Arterial blood always contains a larger proportion of carbonic acid than of oxygen, even during apnoea. This proportion is diminished by depletion, by elevation of the internal temperature of the body; it is increased after digestion, anæsthesia, and by lowering of the external temperature. It is more abundant in the blood of the large arteries, and during asphyxia may reach the amount of 52 vols. per 100 vols. of blood.

Nitrogen.—This gas appears to exist in blood in a state of

simple solution, and in the same proportion in all kinds of blood. Its variations have not, however, been very carefully studied.

Differences between Arterial and Venous Blood.—The following table (from Beaunis) shows the chief characteristic differences :—

	Arterial.	Venous.
<i>Color</i>	Vermillion.	Dark red (modena or purple) ; dichröic.
<i>Coagulation</i>	More rapid.	Less rapid.
<i>Gases</i>	More oxygen.	Less oxygen.
	Less carbonic acid.	More carbonic acid.
<i>Corpuscles</i>	Fewer red corpuscles.	More red corpuscles.
	More water.	Less water.
	More fibrin.	Less fibrin.
<i>Composition</i>	More salts.	Less quantity of salts.
	More extractive matters.	Less quantity of extractive.
	Less fat.	More fat.

Arterial blood presents an almost uniform composition everywhere throughout the body ; venous blood, on the other hand, differs according to the organ from which it returns. The blood in the left side of the heart contains a larger proportion of white corpuscles than that on the right, which has been accounted for by the dilution of the venous blood by the current of lymph and the concentration of blood in its passage through the pulmonary capillaries.

Blood of capillaries remains fluid after death, and does not coagulate even when exposed to the air (Virchow). This peculiarity may be explained by the passage of the fibrinogen by transudation into the tissues.

Blood of Vena Porta.—The blood of this vein must obviously vary according to the period of digestion and the state of the alimentary canal. The following table (from Drosdoff) gives a comparative analysis of portal and hepatic venous blood :—

	Portal.	Hepatic.
Water	725.80	743.39
Solids	274.20	256.61
Haemoglobin, albuminoids, and insoluble salts	251.75	237.88
Cholesterin	2.59	2.73
Lecithin	2.45	2.90
Fat	5.75	.97

	Portal.	Hepatic.
Alcoholic extract . . .	1.27 ...	1.36
Aqueous extract . . .	5.05 ...	5.68
Mineral salts . . .	5.38 ...	5.07
K ₂ SO ₄ . . .	.17 ...	.13
KCl . . .	.66 ...	.61
NaCl . . .	2.75 ...	2.84
Na ₂ HPO ₄ . . .	.63 ...	.55
Na ₂ CO ₃ . . .	.53 ...	.46

According to this analysis the blood of the vena portæ contains more solid matters, more fat, more mineral salts (especially sodium phosphate), and, at the same time, less cholesterin and lecithin than that of the hepatic veins. The portal blood contains but mere traces of sugar. It coagulates more quickly than the blood of the right side of the heart; the clot is softer and more diffuent, containing less fibrin, and this fibrin, when exposed to the air, liquefies at the end of 12 hours (Beclard).

Blood of the Hepatic Veins.—Besides the differences already given, the blood of the hepatic veins contains more corpuscles than that of the portal vein. The following are the proportions found in the dog :

Blood of hepatic veins . corpuscles, 69.73 . plasma, 30.27
Blood of vena portæ . . . „ 45.22 . . . „ 54.78

The proportion of white to red corpuscles is 1 : 170 (Lehmann). According to Lehmann, fibrin is not present, and hence this blood does not coagulate after death; but David states that he has obtained fibrin to the amount of 6 or 8 per 1,000 parts, whilst the portal venous blood contains but 2 to 4 parts per 1,000. Schiff, Valentin, and others, also affirm that hepatic venous blood does coagulate. It always contains an appreciable amount of sugar. The color is a deep violet.

Blood of the Splenic Vein.—The testimony of observers on this head is found to be rather conflicting. Beclard found a diminution of red corpuscles; Malassez, by more reliable methods of calculation, has reported an increase. According to most authorities, the proportion of white corpuscles is increased : 1 : 102 red (Preyer); 1 : 70 (Hirt); 1 : 4.9 (Vierordt); 1 : 3 (Funke). Tarchanoff, however, asserts that all those calculations are erroneous, and that the proportion is not greater than in the blood of the splenic artery. The corpuscles are often dentate, and sometimes contain crystals; this blood easily yields crystals. The amount of fibrine has been found increased (Gray, Funke); diminished (Lehmann). A large proportion of cholesterin is present (Funke, Marcet).

Blood of the Renal Vein.—This blood is richer in oxygen and poorer in carbonic acid than that of the artery (Mathieu and Urbain); it contains less water, chloride of sodium, creatine, uric acid, and urea; it coagulates slowly and imperfectly; it is also rutilant.

Menstrual Blood.—It was formerly believed that this blood was deficient in fibrin, but this idea has been disproved: the mixture of vaginal mucus usually prevents coagulation. The clot is soft and diffuent.

Influence of different states of the organism.—(1) *Age.* The blood of the early embryo does not coagulate. The number of red corpuscles is more

considerable than in that of the adult, and the size is smaller (Berchon, Périér). At birth the proportion of blood is $\frac{1}{4}$ th the weight of the body, instead of $\frac{1}{5}$ th, as in the adult. The blood of the foetus of fifteen weeks forms, at the end of from two to four days, a soft fibrinous clot, and its coagulability gradually increases. Some time after birth the corpuscles diminish in proportion, but increase again at puberty. Another diminution takes place in old age, when the blood is also found to contain more water, fibrin, salts, and cholesterin; the quantity of oxygen decreases towards either extreme of life.

(2) *Sex*.—The blood of the human female contains fewer corpuscles and less hæmoglobin, and is, therefore, less highly colored; its specific gravity is less, it contains more water, less albumin, fats, and extractive matters.

(3) *Stature*.—The proportion of blood has been said to be in inverse ratio to the stature (Welcker). It is small in fat people, in those of feeble constitution, and less in the inhabitants of cities than in those who live in the country.

Influence of the different functions.—(1) *Alimentation*. Inanition has been asserted by Panum and Valentin to have no appreciable effect on the ratio of the quantity of blood to the weight of the body—in contradistinction to the previously received opinions of Chossat, Bidder and Schmidt, Collard de Martigny, &c. Nor has it any notable effect on the composition of the blood. In the dog a slight diminution of the hæmoglobin has been found (Subbotin). According to other observations it increases the quantity of water and of salts, and diminishes all the other principles, including the oxygen. The white corpuscles rapidly diminish, and in the frog have even been found to disappear altogether (Kölliker). Imbibition of fluids does not markedly increase the proportion of water; but complete want of drink causes a diminution, with a relative increase of the coloring matter. An animal diet increases the proportion of corpuscles, of fibrin, of extractives, and of salts, especially phosphates and those of potash; by the use of vegetable food, on the other hand, the blood becomes more watery; the albumin, sugar, and fats increase; and the calcium and magnesium salts predominate. During the use of fatty food the serum is found to be loaded with fat, so as to present an almost milky appearance; amylaceous substances increase the proportion of sugar. The blood of carnivora is richer in phosphates; that of herbivora abounds in carbonates, and succinic acid is also present.

Digestion increases all the constituents of the blood except (according to many authorities) the quantity of water; others assert that the total quantity of blood is greatly increased. The number of red corpuscles is increased after a meal, is at its maximum at the end of about an hour, then diminishes gradually during the next six hours. The white corpuscles also increase during digestion, as is shown in the following table (after Hirt):—

Morning	1 : 1761
Half an hour after the first meal ..	1 : 1695
Two and a half to three hours after ..	1 : 1514
Half an hour to an hour after mid-day meal ..	1 : 429
Two and a half to three hours after ..	1 : 1481
Half an hour to an hour after the evening meal ..	1 : 544
Two and a half to three hours after ..	1 : 1227

The increase of the white corpuscles commences thirty minutes after a meal, and continues for two hours after (Pury), and the curve of the increase corresponds pretty closely to that given by Litchensfeld and Frölich of the increase of pulse and temperature. During digestion there also occurs a diminution of the oxygen and an increase of the carbonic acid of arterial blood; this change attains its maximum about four hours after a meal, and the blood does not regain its normal type till about eight hours after (Mathieu and Urbain).

(2) *Muscular Exercise*.—Contradictory conclusions have been arrived at on this head by different observers. Mathieu and Urbain, by more carefully-conducted analyses have ascertained a slight increase of the oxygen of arterial blood, and a diminution of its carbonic acid during muscular exercise. This change is probably due to increased frequency and depth of the respiratory movements.

(3) *Pregnancy*.—Becquerel and Rodier found in the later months of pregnancy a diminution of corpuscles and of albumin; water was found to be increased, and a slight increase of fibrin was also ascertained. Nasse also found a diminution of the soluble salts, and an increase of fat. During lactation the fibrin was found to be greatly diminished; the soluble salts at first increase, then diminish; the iron was found to be in larger proportion.

(4) *Sleep*.—The oxygen of arterial blood is diminished during sleep, probably on account of the diminished activity of the respiratory movements.

(5) *Respiration and Circulation*.—Increased frequency and depth of the respiratory movements increase the proportion of oxygen in arterial blood; increased velocity of the circulation has the opposite effect.

Influence of external agents.—*Heat* increases the proportion of oxygen in arterial blood, and diminishes that of the venous; the carbonic acid is diminished in both. *Cold* increases the carbonic acid of arterial blood, and diminishes the oxygen of both kinds of blood (Mathieu and Urbain).

SERUM.

Pure serum may be obtained by merely allowing the blood to clot and then pouring off the fluid, or better, by placing the vessel containing the clotted blood in an apparatus furnished with a horizontal centrifugal movement. Obtained in this way serum is found to be a transparent fluid, almost quite clear, with a slight yellowish-green tint. Its alkalinity is somewhat better marked than that of plasma. After a meal rich in fatty food, it presents a milky appearance, due to the presence of enormous numbers of fat globules. A special pigment gives the normal tint to serum, and this is probably deepened by a small quantity of dissolved hæmoglobin. The serum of the ox is quite colorless, that of the rabbit is nearly so, while that of the dog is almost identical in color with that of man. Horse's serum has a distinct yellowish amber tinge. The specific gravity of the serum of human blood is 1028 (1027—1029).

The chemical analysis of serum demonstrates the presence of the following substances :—

(1) *Albuminoids*.—Serum-albumin, albuminate of soda, and an excess of paraglobulin which remains after coagulation of the plasma. Their proportion varies from 7 to 10 per cent.

(2) *Nitrogenous compounds*.—Urea (.02 per cent. of total quantity of blood), creatin (Voit); and small quantities of inconstant constituents: uric acid, creatinin (?), hippuric acid (Verdeil, Goldfuss), carbamic acid (Drechsel), sarcin, xanthin, leucin, tyrosin, trimethylamin, ammonia. The latter is probably due to the decomposition of some ammonical salt.

(3) *Non-nitrogenous compounds*.—Glucose (.051 per cent. of total quantity of blood); neutral fats (.1—2 per cent.); in the form of an emulsion; soaps of the fatty acids; cholesterin (.02—.03 per cent.); organic acids, especially lactic, and, perhaps, volatile fatty acids (acetic, butyric, caproic, &c.); alcohol (?), &c. Sarcolactic acid has been found by Spiro, and succinic acid by Meissner.

(4) Lecithin.

(5) A special pigment, believed by some to be hydrobilirubin, by others to be a product of oxidation of hæmoglobin; *cholepyrrhin* has been discovered in horse's blood.

(6) An amylolytic ferment analogous to ptyalin.

(7) Inorganic salts; chlorides, sulphates, phosphates, and carbonates of sodium, potassium, calcium, and magnesium; traces of manganese. Soda, salts, and chlorides predominate in the serum, phosphates and potash are in the largest proportion in the corpuscles as already seen.

(8) Water (about 90 per cent.)

(9) Gases.—The proportions we have already examined.

IV. FORMATION OF THE CORPUSCLES.

The first appearance of blood corpuscles in the human embryo is in the middle germinal layer (mesoblast), where they are formed by pigmentation and differentiation of some of its cells. These cells then rapidly multiply by fission. These early red corpuscles accordingly are possessed of nuclei; afterwards the non-nucleated corpuscles begin to appear. In the human embryo of 30 mm. in length, half the red corpuscles are without nuclei. In the embryo of four months, a nucleated red corpuscle appears but occasionally. As soon as the liver is formed, the red corpuscles are generated there, and the production by fission ceases (Kölliker). Later on they are formed from the white corpuscles which become impregnated with hæmoglobin, the nucleus disappearing at the same time. Some observers, indeed (Wharton Jones, Huxley, &c.), believe that it is the nucleus itself which subsequently forms the red corpuscle. The chief argument in favor of this view is

the nearer correspondence in size, in most of the mammalia, between the red corpuscle and the nucleus of the pale. Semmer, as already mentioned, looks upon the "red granular corpuscles" as an intermediate form between the pale and red. Hayem takes a different view of the development of the red corpuscles from those of previous observers, and describes the progenitor of the latter as a distinct form of colorless corpuscle, to which he has given the name of *hæmatoblast*. The researches of Ponchet have led him to believe that both red and pale corpuscles are developed from a common nuclear element (*noyau d'origine*). It is a spherical nucleolated mass which either enlarges to form a leucocyte, or develops into a red corpuscle by pigmentation.

Schäfer describes a formation of red corpuscles from connective tissue corpuscles by differentiation of the protoplasm.

In the adult spleen small nucleated colored corpuscles have been observed similar to those of the embryo, and also corpuscles apparently in the transition stage between white and red, showing partial pigmentation with commencing degeneration of the nucleus. Similar cells have been observed in the wide capillaries of the red marrow of bones, the hæmatogenous function of which was first pointed out a few years ago by Neumann.

The origin of the white corpuscles is probably in adenoid tissue in all the different situations in which the latter is found throughout the body. They also multiply by division, as has been observed by Klein. This observer has likewise seen them budded off from the reticulum of the spleen.

Fate of the Corpuscles.—There can be little doubt that the destiny of a large proportion of the white corpuscles is to form red; a considerable number also "migrate" through the capillary walls into the extravascular parts of the tissues, where their subsequent course is unknown. Probably a large quantity break up in the blood and disappear.

With regard to the red, the great seat of their destruction seems to be the spleen, in which, as Kölliker was the first to observe, large numbers of these bodies may be seen in various stages of disintegration.

CHAPTER VI.

CIRCULATION OF THE BLOOD.

In order that the blood should fulfil its physiological functions, it is absolutely necessary that there must be an unintermitting flow of this fluid through all parts of the body, so as to keep it in close contact with the various tissues. The fact that the blood does circulate in a continuous stream through the vessels was discovered for the first time by William Harvey (1619). He did not publish his discovery till nine years afterwards (1628), as he dreaded the opposition of his contemporaries, which he knew was sure to be called forth by the announcement. The chief proofs on which he relied were the phenomena observed during venesection, then a common operation. He saw that the vein swells below the ligature, and the blood flows from the side of the orifice furthest from the heart—the contrary occurring in case of an artery. The direction of the valves of the veins, already demonstrated by his former master, Fabricius ab Aquapendente, was also an argument in favour of the novel discovery. Harvey was not, however, aware of the existence of capillaries, but believed that the blood, after leaving the small arteries, permeated the various tissues, to be taken up on the opposite side by the open mouth of the veins.

The circulatory apparatus consists of :—

(1) The heart beating rhythmically and propelling by each contraction a definite quantity of blood into the aorta (and pulmonary artery).

(2) The arteries furnished with muscular and elastic coats, to provide for accommodation of the added quantities of blood, and to regulate the amount distributed to the different parts of the body.

(3) The capillaries of minute calibre, furnished with walls of extreme tenuity, and not only quite permeable to the liquid parts of the blood, but also allowing the corpuscles to pass through.

(4) The veins, whose use is chiefly passive, conveying the blood back to the heart from the various tissues. The coats are similar to those of the arteries, but much thinner, and they are also supplied with valves.

The Heart.

The heart is a hollow muscular organ, the external surface of which is covered by a fibro-serous membrane, the pericardium. The lining membrane is called the endocardium. It is placed in the middle mediastinum, and somewhat to the left side. The shape is conical, and a point a little above the apex produces the impulse, which may be seen and felt in the healthy chest in the fifth left intercostal space, and half way between the mammillary and parasternal lines.

In the adult the heart is completely bilateral, the right and left sides being completely separated by a septum. The right side of the heart presides over the *pulmonary circulation*, by which the blood is sent through the lungs to be exposed to the air. The left side presides over the *systemic circulation*, by which the blood is sent to all parts, to convey nutriment to the various tissues, and remove the products of metamorphosis.

Structure of the Heart.—The muscular tissue of the cardiac walls differs markedly from involuntary muscle fibre found in other organs of the body. The fibres (Fig. 13) present striations like those of voluntary muscle, but less regular, and not so well pronounced. They possess no sarcolemma, are smaller than those of voluntary muscle, and vary greatly in thickness. Careful preparation shows the cardiac fibres to be made up of quadrangular cells, which give off processes to meet with those of neighboring cells, and so limit spaces which transmit the plasma of the blood, sometimes lymphatic or blood capillaries. Near the centre of each cell is found a well-defined oval nucleus (sometimes two are present). Beneath the endocardium in many animals, and in the human heart during fetal life, there may be found a layer of greyish bundles of muscle fibres, discovered by Purkynie, and since known by his name. Kölliker has found among these, many fibres closely approaching the structure of voluntary muscle.

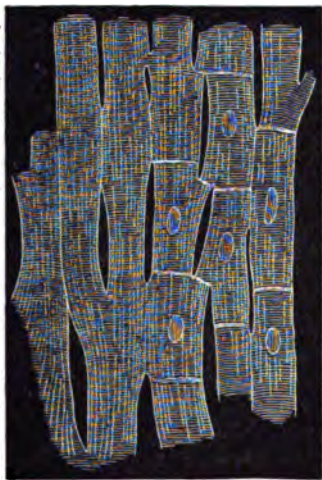


Fig. 13.

Among the elastic lamellæ of the endocardium, Schweigger-Seidel has found scattered bundles of smooth muscle cells.

In adult life the heart forms a double organ, a complete septum separating the right from the left side. The right side presides over the so-called *pulmonary circulation*, by which the blood is sent through the lungs, where the necessary interchanges take place between it and the atmospheric air. The left side presides over the systemic circulation, by which the blood is sent to all the various parts of the body, to convey the materials for the nutrition of the tissues, and to remove the products of retrograde metamorphosis. Each side of the heart consists of two cavities, an auricle and a ventricle, and the opening between the two, which is surrounded by an unyielding fibrous ring (*zona tendinosa*), is guarded by a strong valve.

Leaving the left ventricle, the blood passes along the arteries into the capillaries, which, in their turn, converge to form the venous canals; these convey the blood back to the heart, and thus is completed the *systemic circulation*. Entering the right auricle of the heart, the blood thence passes into the right ventricle, by which it is propelled along the pulmonary artery to the lungs, and after passing through the pulmonary capillaries, it returns, oxygenated and purified by its exposure to the air, along the pulmonary veins, to the left auricle. Passing thence into the left ventricle, it recommences the same round again.

The continuous current of blood is maintained by the difference of the intravascular pressure in the various segments of the circuit along which it has to pass. The function of the heart, as the great central organ of the circulation, is simply to maintain this inequality of pressure.

MOVEMENTS OF THE HEART.

In the pericardial cavity the movements of the heart are facilitated by the serous sac, of which the parietal layer lines the fibrous pericardial wall, while the visceral layer is reflected over the surface of the heart. Below, the pericardium is adherent to the diaphragm, of which it limits the ascending and descending movements, while above it is lost on the sheaths of the great vessels, which are so far fixed in position as to be able to limit effectually any considerable movement in this

region. From the want of elasticity of its fibrous investment, the pericardial cavity cannot change its capacity to any considerable extent in the normal state of things.

The heart, like the other intra-thoracic organs, has a tendency to dilate, in consequence of the negative pressure to which its external surface is exposed. The internal surface of the heart and of the intra-thoracic vessels is exposed through the intervention of the contained blood to a pressure equal to that of the atmosphere (760 mm.), and to this must be added the negative pressure due to the elasticity of the lung tissue (varying from 6 to 40 mm.)

The movements of the heart of a living animal may be studied by removing the chest wall, and maintaining artificial respiration. On opening the pericardium, the rhythmic contraction is seen to commence in the walls of the *venæ cavæ* and pulmonary veins, a peristaltic wave beginning at some distance, and increasing in intensity as it approaches the auricles. The wave of contraction then rapidly passes over the auricular walls, from the mouths of the veins towards the auriculo-ventricular opening. The appendicular contraction seems to complete the auricular systole, which is extremely rapid.

The contraction of the ventricles immediately succeeds to that of the auricles ; it is less rapid than the auricular systole ; the whole of the ventricular wall contracts at the same moment, and the ventricles are seen to become shorter and thicker. The heart rotates slightly on its long axis from left to right, so that the apex moves forward and to the right side, and more of the left ventricle is exposed to view, while the base remains comparatively fixed. The aorta and pulmonary artery are at the same time seen to expand and become elongated, from the increased volume of blood. During systole the ventricular portion of the heart becomes more regularly conical with circular base, having presented during diastole the form of a flattened cone with elliptical base ; the base is drawn downwards, the apex upwards, and the sides inwards, all towards a central point. The transverse diameter is shortened, while the antero-posterior diameter of the base is increased. The circumference of the base is increased during the ventricular systole (Kürschner).

The diastole of the auricle commences simultaneously with

the systole of the ventricle. The blood flows from the veins into the former cavity as soon as the relaxation of its walls allows them to yield passively to the tension of the column of blood within the veins. During the ventricular systole the contraction of the muscoli papillares has a peculiar effect in increasing the size of the auricular cavity, as pointed out by Küss. The cone-shaped prolongation of the auricle, which is formed by the auriculo-ventricular valve, is widened and elongated by the contraction of the papillary muscles, which has the effect of approximating the cusps of this valve to the wall of the ventricle. The free edges of the valves, meeting at the same time, prevent regurgitation into the auricle, and the whole acts the part of a hollow piston which ensures the complete emptying of the ventricle, while the enlargement of the conical prolongation of the auricle has the effect of aspiration.

The function of the auricle obviously is to act the part of a reservoir, which accommodates the blood during the contraction of the ventricle, and so maintains the medium pressure of the blood in the veins. Regurgitation does not take place under the normal conditions, being prevented by the direction of the peristaltic wave of contraction, which passes from the venous towards the auriculo-ventricular openings. On this account no valves are necessary to guard the mouths of the veins. The pressure of the column of blood in the latter vessels also offers some resistance.

When the ventricle has ceased to contract, the blood easily passes from the auriculo-ventricular cone into the ventricle, the cavity of which dilates till the pressure becomes equal in the two chambers. Some observers have attributed a suction power to the wall of the ventricle, by its elastic recoil after the cessation of the systole; most authorities, however, believe that its dilatation is purely passive, but allowing some influence to the negative external pressure. Goltz and Gaule have demonstrated, by the aid of the *minimum manometer*, a negative pressure of -17 in the right ventricle immediately after the cessation of the systole, and of -52 in the left. Marey had previously shown that a lowering of pressure existed at the end of the ventricular systole (*vacuité post-systolique*).

The obvious change in the relations and supports of the heart after the thoracic cavity has been opened, has led to the making

of other experiments for the purpose of studying the movements of the organ in the unopened chest. If three needles be passed through the chest wall perpendicularly, and into the ventricle, one at the apex, one at the base, and a third half-way between the others, they will be found to move with the beats of the heart. The head of the uppermost needle moves suddenly upwards to a considerable distance, whilst that which passes through the apex merely quivers. The head of the middle one moves upwards, but to a less distance than the first. This shows that the apex of the heart retains its place during systole while the base moves downwards, and is explained by the elongation of the great arteries and the shortening of the heart to a precisely similar extent. The needles, after the death of the animal, will be found with their heads all directed downwards, showing that the whole ventricle has ascended with the contraction of the aorta and pulmonary artery.

Cardiac Impulse.—The shock or impulse produced by each beat of the heart can be seen and felt, as we have already mentioned, in the fifth left intercostal space, and half-way between the mammillary and parasternal lines. Its area in health is about a square inch. The impulse may also be felt through the diaphragm after passing the finger through an incision made in the abdominal wall.

Various attempts have been made to explain the impulse of the heart, the causation of which had been apparently involved in needless mystery till within a late period. It was believed by Reid to be due to the mechanism of a bundle of spiral fibres, which he described, placed on the anterior surface of the heart, and the effect of whose contraction he considered to be to tilt forward the apex, and so produce the impulse. The *recoil* theory of Hiffelsheim, which compares the impulse of the heart to the recoil of a gun, or of an hydraulic tourniquet, after discharging its contents, has been adopted by many high authorities (Guttbrod, Skoda, Robin, Guttmann, Jahn). The chief argument of Hiffelsheim in support of this theory is, that ligation of the great vessels at the base of the heart suppressed the impulse more or less completely. But the same argument has been adopted by Kornitzrer in support of his theory, that the impulse is due to a systolic torsion of aorta and pulmonary artery into a spiral form. The explanation of Senac, which has been renewed of late years by Ludwig, is that

the aorta straightens itself by a kind of lever movement each time that a column of blood was thrown into the vessel and so tilted the apex of the heart forwards.

But the chief cause of the impulse undoubtedly is the sudden change in the shape of the heart and the hardening of its fibres. The almost instantaneous rapidity with which it passes from a state of flaccidity to one of extreme tension, can be best perceived by holding the heart between the fingers during the systole.

The effect of the ventricular systole on the position of the apex is well represented in the accompanying diagram (after Rollett). The form and position of the heart during diastole is figured, while the dotted lines point to the position of the apex and limits of base at the moment of extreme ventricular contraction.

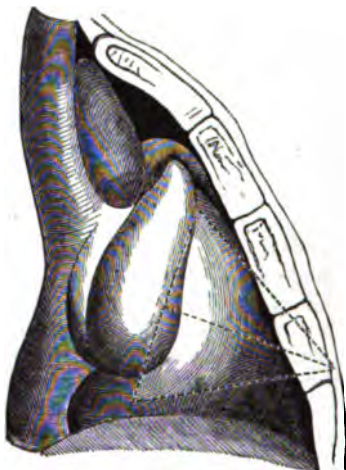


Fig. 14.

In order to study as fully as possible the movements of the heart various modes of exploration have been adopted.

(1) The simplest mode of examining the action of the heart after inspection of the chest wall, is by the application of the hand—*palpation*. In a few cases an opportunity has been afforded of examining the heart more directly: wound of the precordial region (Bamberger),

congenital fissure of the sternum (case of Groux), absence of sternum with ectopia cordis (case of François-Franck).

(2) *Direct Inspection*.—The movements of the heart have been *seen* in cases of executed criminals and in the foetus. At Boston the heart of a criminal was exposed after hanging, and was observed to beat for four hours.

(3) *Graphic Method*.—This method has been applied for the purpose of studying the movements of the heart by Marey and others. The clinical cardiograph of Marey (*explorateur à aquille*) is formed of an elliptical wooden capsule of which the margins are applied closely to the surface of the chest; from the bottom of the capsule projects a spring, which can be made more or less tense as may be convenient, and this is armed with an ivory plate, which presses upon the point where the impulse is felt. The movements transmitted to the air within the capsule by the cardiac pulsations are communicated to a lever by means of a tube furnished with a tambour.

Another cardiograph is made by applying to the chest at the point of the apex beat the tambour of the stethoscope of Kœnig, which is a small tambour closed on one side by a double elastic membrane, which after the insufflation of air encloses a lenticular space; the other end of the tambour communicates with a tube which terminates by a ferrule. This tube is placed in connection with a tambour, furnished with a lever, which is raised by each pulsation of the heart, and the movements of which are then transmitted to a recording cylinder. The wood-cut shows a tracing obtained by this instrument.



Fig. 15.

Tracing of the cardiac movements in man (Marey).

The *explorateur à tambour* of Marey is still more convenient. The interior of a bell-shaped piece of wood, of which the summit is perforated by a tube, contains a capsule of metal, which communicates with the tube. The base of the capsule is closed in by a thin caoutchouc membrane, and it encloses a delicate spiral coil of wire which makes the membrane to project by its pressure. An aluminium disk and a cork button rest on that membrane. The slightest pressure on this button drives the air out of the capsule into the tube and on to the register-

ing apparatus. A graduated scale shows the amount of pressure exercised on the button.

Galabin has modified the *sphygmograph* of Marey for application to the precordial region. The *polygraph* of Mathieu and Meurisse and the *pansphygmograph* of Brondgeest are instruments constructed on the same principles as the *cardiograph à tambour* of Marey. The principle of the manometric flames of Kœnig has also been applied (by Landois, Gerhardt, &c.) for the purpose of making visible the cardiac pulsations.

(4) *Cardio-pneumatic Movements*.—Voit and Losser observed some years ago that on account of the diminution of the volume of the heart during the ventricular systole, a rarefaction of the pulmonary air occurs which, if respiration be suspended at the moment, causes an opening of the glottis. Accordingly, if a tube communicating with a *tambour*, and furnished with a lever, be placed between the lips, a tracing will be obtained exactly corresponding to a reversed cardiac, the descent of the cardio-pneumatic curve corresponding to the ascent of the cardiographic, and *vice versa*. These relations have been studied by Ceradini and Landois with the aid of special instruments (*hamathoracograph* of Ceradini, *cardiopneumograph* of Landois).

In the lower animals still more searching means of examination have been employed. The cardiograph of Chauveau and Marey for intra-cardial exploration (an improved form of that of Buisson) consists of a small ampulla made of caoutchouc, which is introduced into the cardiac cavity of which the pressure is sought, and which communicates with a *tambour à levier*. Three of the four cavities of the heart have been explored in this way: the right auricle and ventricle through the internal jugular vein and vena cava superior, the left ventricle through the left carotid and aorta. The left auricle alone is inaccessible.

During the ventricular systole the contained blood is pressed

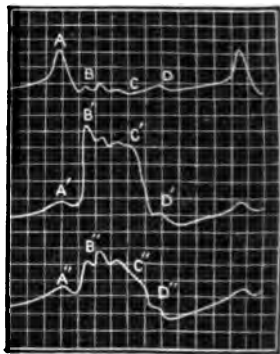


Fig. 16.

Tracings obtained by Chauveau and Marey's apparatus:—

(A B C D)—Auricular Tracing.
(A' B' C' D')—Ventricular do.
(A'' B'' C'' D'')—Impulse do.

between the ventricular wall and the auricular cone (already described) by the action of the *musculi papillares*; this has the effect of securing the more complete emptying of the ventricular cavity. Nevertheless, according to Chauveau and Favre, a small quantity of blood remains, forming a kind of dome around the auricular cone, which can be felt by introducing the finger into the auricle. This was done in case of a horse killed by section of the medulla oblongata, artificial respiration being afterwards maintained during the experiment.

The pressure of the blood during systole causes the edges of the auriculo-ventricular valves to come into contact and prevent any regurgitation of blood into the auricle. The closure is sudden and complete, and effectually prevents any reflux. This may be demonstrated, as was shown long ago by Lower, by exposing the auricular surface of either valve while water is injected into the ventricle through the aorta or pulmonary artery. Not a drop passes into the auricular cavity on either side. The extreme thinness of the margins of the valves allows the adjacent borders to fall into complete contact with greater ease, while the anatomical arrangement of the *chordæ tendineæ*, which pass from the apices of the same papillary muscles to the edges of adjacent flaps, secures the more perfect apposition.

The above considerations lead us to reject the so-called "*safety-valve function* of King," by which the over-distended right ventricle was supposed to allow the escape of part of its contents back into the auricle, thereby preventing the paralysis of distension.

The *semilunar valves* are thrown upwards by the column of blood emerging from the ventricular cavities, which also widely distends the elastic aortic arch, already overfilled with blood. When the contraction of the ventricular wall has ceased, the elastic walls of the aorta recoil upon their contents and press down the column of blood, a part of which, passing into the pouches behind the sigmoid valves (so-called *sinusæ of Valsalva*), rapidly shuts them down, so as to prevent any reflux. The flexibility of the *lunula* allows the edges to fall into more exact apposition (as Sir Thomas Watson has specially pointed out), and the *corpora Arantii* are believed (at least by some) to fill up the central interval, where otherwise a triangular space would have been left. On account of the greater width of the aorta above the opening, a great part of the momentum

of the recoiling column of blood is borne by the tendinous zone which surrounds the arterial orifice, and by the ventricular wall, and this arrangement saves the semilunar valves from what might otherwise prove too great a strain.

Whether the semilunar valves cover the openings of the coronary arteries during the ventricular systole, and so prevent these vessels from receiving their supply of blood till after the commencement of the diastole, is still an unsettled question. It was long ago asserted by Thebesius, and has been powerfully advocated in the present day, by Brücke. Some believe it to be anatomically impossible, and Ceradini, who has *watched* the valves through a glass tube passed into the aorta, says that the semilunar valves are not closely applied to the interior of the aorta during systole. The systolic squirt of blood from a wounded coronary artery Brücke explains by the increased pressure produced by the compression of the contracting muscular fibres on one side, and the increased tension within the aorta on the other, the reversed conditions preventing an active flow during diastole. Brücke has also shown that, if the heart be held in a proper position, a stream of water passes from the pulmonary veins into the auricle and through the ventricle into the aorta, without a drop passing into the coronary arteries. This experiment has, however, been said to be equally successful when the semilunar valves are absent. Another experiment, and one not so easily gainsayed, is the following by Klug:—by stimulation of the vagus the heart's action has been slowed, so as to make it quite easy to detach the heart from its connections during systole or diastole, according to the wish of the observer; in hearts removed from the body in this way, and immediately plunged into dilute sulphuric acid, so as to coagulate the blood, subsequent examination always showed that the heart removed during systole presented vessels but poorly filled, whilst that removed during diastole had all its vessels widely distended.

Brücke has claimed for this diastolic injection of the coronary arteries the additional advantage of causing a somewhat active dilation of the cavities, attributing, in this way, the various movements of the heart to a kind of *automatism* (Selbststeuerung).

Duration of the phases of a cardiac cycle.—The following table gives (after Gibson), the duration in fractions of a second

of the different periods of contraction and relaxation of the cardiac walls :—

			Maximum.	Minimum.	Mean.
Auricular systole	..	..	.130	.100	.112
Ventricular	..	..	.395	.325	.368
Diastole and repose of heart	..	..	.690	.455	.578
Total duration	..	..	1.190	.925	1.057

Sounds of the Heart.—Auscultation of the precordial region discovers the production of two sounds : the first a prolonged, dull, and booming sound ; the second, short and sharp. They may be compared to the syllabic sounds, *lubb* and *dupp* respectively (Williams). The points at which they are best heard are :—*First sound*, for left ventricle—at point of impulse ; for right ventricle—the point of articulation of fifth right costal cartilage with sternum : *second sound*, for aorta—point of inarticulation of second right costal cartilage with sternum ; for pulmonary artery, the inner end of second left intercostal space.

Between the first and second sounds the interval of time is hardly appreciable, but a very distinct pause intervenes between the termination of the second sound and the commencement of the first.

With regard to the causes of these sounds, whilst that of the second has been satisfactorily demonstrated, that of the first is still the subject of controversy. It was attributed long ago by Magendie to the stroke of the heart against the chest wall ; but this explanation is untenable, as the sound persists when the chest wall has been removed, or even after the removal of the heart from the body. The theory of Halford and Billing, that it was due to the tension of the auriculo-ventricular valves, has been controverted by Ludwig and Dogiel, who have shown that the sound persists in the heart of a curarised dog, removed from the body even when the latter is emptied of blood, and the valves on that account cannot be made tense. The other prominent idea—that it is no other than the *bruit musculaire*, produced by the contracting fibres of the cardiac wall—has been met by the objection that a single spasmodic contraction cannot produce a musical note,

such as the first sound of the heart is. Wintrich believes that the sound is partly due to each of the two latter causes, and has endeavoured to isolate the muscular from the valvular element by the use of a resonator (*polyscope*), formed by a truncated cone of zinc, over the mouth of which a thin caoutchouc membrane is spread, and so arranged that the tension may be regulated to any required degree. According to the degree of tension of the membrane there will be heard either the longer and deeper sound due to the *bruit musculaire*, or the shorter and sharper note produced by valvular tension.

There can be no doubt that both factors contribute to the sound, and if we recollect, as Küss observes, the manner in which the valvular tension is maintained by the contraction of the papillary muscles, its production becomes less difficult to comprehend.

The events taking place within the heart during the respective sounds may be tabulated as follows:—

<i>During first sound.</i>	<i>During second sound.</i>
Ventricles contract.	Ventricles dilate.
Auricles dilate.	Auricles dilate.
Auriculo-ventricular valves are made tense.	Auriculo-ventricular valves open.
Aortic and pulmonary valves opened, and blood passing through the openings.	Aortic and pulmonary valves closed.
Impulse takes place.	

The cause of the second sound has been clearly shown, as first suggested by Rouanet (1832), to be due to the tension of the semilunar valves of aorta and pulmonary artery.

Mechanical work of the Heart.—To calculate the average quantity of blood ejected from the ventricle during each systole various methods have been employed. The one employed by Santorini, and in the present day by Dogiel, is by filling the ventricle with blood or other fluid of known density up to the condition of normal dilatation. Abegg opens the thorax of an animal, and applies ligatures around the origin of the great vessels, rapidly tying them at the time of repletion of the heart, which is then removed and weighed. The blood is then allowed to escape, and the empty heart is weighed. The method of Hiffelsheim and Robin is by taking moulds of the various cavities

of the heart with wax, and measuring the latter by the amount of water which they displace. Volkmann and Vierordt, knowing the sectional area of the aorta, and the rate of the current of blood in that vessel, calculate the amount passing into it per second, and allowing a systole plus one-fifth for each second, calculate in this way the amount ejected from the ventricle at each systole.

The mean of the various estimates which have been made gives 6 oz. (180 grammes) as the quantity of blood ejected from the ventricle at each systole. It is obvious that the quantities emitted by each ventricle must be identical: if a larger amount passed out of the left ventricle, the blood would rapidly accumulate in the systemic circulation; if a larger quantity were ejected by the right ventricle, accumulation would take place in the lungs.

The pressure in the human aorta has been calculated to equal that of 20 centimetres (8 inches) of mercury, or $2\frac{1}{2}$ metres of blood. As the effort of the cardiac contraction is directed to overcome this pressure, the work done at each systole of left ventricle is $180 \times 2\frac{1}{2} = .45$ kilogrammetres. This would correspond to .54 kilogrammetres per second, or to 46,656 kilogrammetres during twenty-four hours. As the pressure in the pulmonary artery is about one-third that within the aorta, the work of the right ventricle would be represented by 15,552 kils., and the total ventricular work of twenty-four hours by 62,208 kilogrammetres, or about one-fifth of the total mechanical work of the organism. The mechanical work so produced by the heart is all converted into heat.

THE CIRCULATION OF THE BLOOD IN THE VESSELS.

The vascular system is so arranged in its distribution throughout the body as to form a double cone, of which one is formed by the arteries and the other by the veins. The bases meet at the capillaries and the truncated apices at the heart. A very short cylinder interposed between the bases of the cones would represent the capillary area. According to Vierordt the sectional area of the capillaries is to that of the aorta as 800:1, and to that of venæ cavæ as 400:1.

The Arteries.—Emerging from the left ventricle of the heart we have a single great vessel, the aorta, the trunk of the

arterial tree, whose branches ramify in all directions throughout the body. At each division of an arterial trunk, at least in case of the smaller arteries, the sum of the sectional areas of the branches is markedly greater than the area of the primitive vessel. The increase is only slight near the centre of the circulation, but near the capillaries the enlargement becomes very rapid. The coats of the vessels which convey the blood are possessed of structural peculiarities, which are of great importance in the maintenance of the flow.

The coats of an artery are three :—

(1). *Tunica adventitia*.—This is composed of condensed connective tissue, comprising finely-felted layers of white fibres placed obliquely, with longitudinal bundles of elastic fibres between. The latter are more numerous near the middle coat (*external elastic coat* of Henle), and are better developed in arteries of larger size, gradually disappearing as we pass down towards the arterioles. Some longitudinal contractile cells have been observed scattered among the layers of this coat, especially in the larger arteries. (2). *Tunica media*.—This consists, in case of the arterioles, of a single layer of smooth muscle-cells placed circularly around the vessel. As the vessels increase in size, the layers multiply, and in the large trunks they are separated by elastic fibres mostly arranged in the form of fenestrated membrane. The proportion formed by these elastic layers increases as the arteries increase in size, and this tissue makes up the great bulk of the middle coat of the aorta. The muscle-cells of the middle coat are seldom more than $\frac{1}{300}$ to $\frac{1}{800}$ of an inch in length, and become shorter in the large trunks. Their margins are very irregular, with jagged (sometimes branched) extremities. In the large trunks a certain amount of connective tissue is also present in the media, "in the form of small branched, flattened, nucleated connective-tissue cells, embedded in a hyaline albuminous interstitial substance" (Klein). (3). *Tunica intima*.—This coat is very distinct in all arteries, and is made up of three distinct layers : (a) a layer of *endothelial cells* laid edge to edge, without overlapping ; the outlines are very indistinct till brought out by the nitrate of silver method of staining, and the nuclei are demonstrated by staining with carmine. (b). A *subendothelial layer*, consisting of longitudinal bundles of connective-tissue fibres, with branched anastomosing connective-tissue corpuscles

lying in the meshes (*inner longitudinal fibrous layer* of Remak and Kölliker). (*c*) *Elastic layers*.—These form the chief thickness of the inner coat. The fibres are mostly arranged in the form of a longitudinal network. The fibres are for the most part broad and flattened, and fused at the edges at intervals so as to form layers of perforated membrane (*fenestrated membrane* of Henle). These layers may be stripped off in small pieces, each of which presents the appearance of a thin and brittle transparent membrane, which possesses a remarkable tendency to curl up at the upper and lower borders.

The presence of the large quantity of elastic tissue which exists in the arterial walls, enables these vessels to expand and receive the blood expelled from the left ventricle at each contraction. By its subsequent recoil it presses on the blood through the capillaries during the period of repose, and so converts the intermittent into a continuous flow.



Fig. 17.

The Capillaries.—The wall of a *capillary* blood-vessel is formed of a single layer of nucleated endothelial cells of fusiform shape, and with outlines smooth or sinuous according to the distension or contraction of the lumen of the vessel. They are united at their edges by an albuminous, semifluid, cementing substance, which in silver-stained specimens appears in the form of dark lines, marking off the outlines of the individual cells. Minute openings (*stomata*) were supposed by Cohnheim to exist between the cells, so as to permit the emigration of blood-corpuscles, but they have no real existence in the normal state.

In the state of abnormal distension which is present in inflammation, the cementing substance gives way in some places, forming minute openings (*stigmata*, Arnold), and these may enlarge to form stomata.

In some places the capillaries have an outer layer made up of branched connective-tissue corpuscles, as in the choroid (Ivanoff, Eberth), or a complete endothelial membrane, as in the pia mater (Axel Key and Retzius), retina (Eberth), and in serous membranes (Klein).

The average diameter of capillaries is about $\frac{1}{2500}$ of an inch. They are small in brain and lung, and still more minute in the retina. The capillaries of the liver are much larger, and those of the medulla of bone still more so.

The Veins.—The coats of veins are similar to those of arteries, but thinner. The adventitia is relatively thick, and the elastic tissue of the media is very scanty. Valves exist, which are formed by reduplications of the intima and partly of the muscular tissue of media. The intima is very thin and elastic, and the endothelial cells lining the interior of the vessel are shorter and broader than in case of the arteries or capillaries.

The adjoining wood-cut shows the arrangement and relative thickness of the coat of an artery (A) and a vein (V). The *tunica adventitia* (a) is known by its relative thinness and areolar structure; the *media* (m) presents in transverse section unstripped muscle cells arranged circularly around the vessel; while the *intima* is formed by the endothelium and the sub-endothelial layers, as already described.

The valves are numerous in the superficial veins of the limbs, few in the deep, and especially in the large ones. They are absent in the portal vein and its tributaries, in the pulmonary, cerebral, and

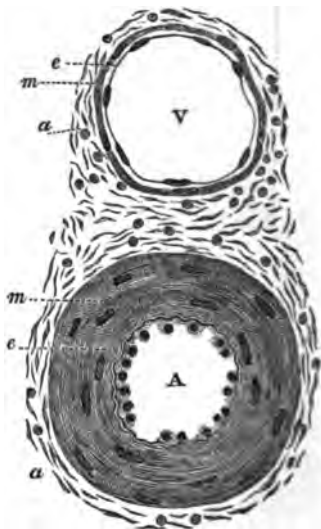


Fig. 18.

spinal veins, and in those veins whose diameter is less than a line.

For the purpose of investigating the phenomena of the arterial circulation many methods of exploration have been devised :—

Sphygmometer of Herison.—This apparatus is formed of a small tube filled with fluid, and having one end bell-shaped, and closed with a thin layer of caoutchouc. This end is placed on the artery, and the pulsations are transmitted to the contained fluid. Naumann has furnished this instrument with a registering apparatus, and given the modified apparatus the misleading name of hæmadynamometer.

Pulsating manometer (of Chelius).—This instrument is similar in construction to that of Herison.

Sphygmograph (Vierordt's).—In this instrument, the predecessor of that of Marey, the pulsations of the artery are noted by the elevation of a lever, the vertical movements of which are transferred to another moving in a horizontal plane. The movements of this instrument are accordingly rather slow, and the tracing obtained shows a line of ascent as long as that of descent, which is misleading. It has been modified by Aberle and by Berti.

Sphygmograph (Marey's).—As in the instrument of Vierordt, the pulsations are recorded by the elevation of a lever, which writes on paper or smoked glass kept moving by clockwork in a horizontal plane. The latest form of the instrument is that of the *sphygmograph à transmission* of this author (represented in the adjoining wood-cut). The vibrations of the

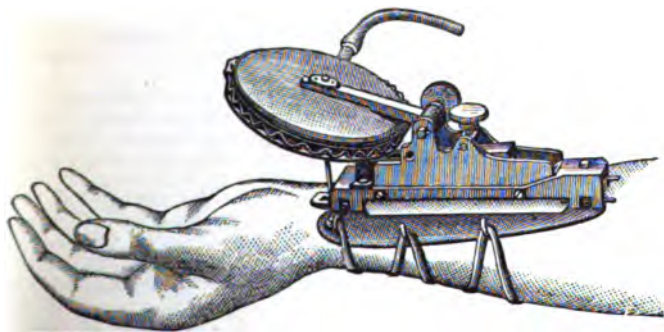


Fig. 19.

lever are here transmitted to a tambour filled with air, from which they are conducted along an elastic tube connected at its other end with the registering apparatus. By this mechanism, tracings of indefinite amplitude may be obtained, but in the form shown in the adjacent figure the object has been to have them of the length of the usual sphygmographic curves.

S. (of Longuet).—In this instrument the pulsations of the artery are transferred by means of a button to a vertical rod, and the vertical movements

of the latter are transmitted by means of a wheel to a pen, which is made in this way to give a tracing (in a horizontal plane) of the movements of the artery on a slip of paper propelled by clockwork.

Pulsuhr (of Waldenburg).—This instrument resembles a good deal that of Longuet, and has additional arrangements for denoting the diameter of the artery, tension, &c.

Polygraph (of Mathieu and Meurisse).—In this instrument a metallic plate is made to press on the artery, by means of a spiral coil of wire, of which the pressure can be graduated. The plate is at the end of a vertical rod, which transmits the pulsation to an air tambour (as in Marey's instrument), and this is connected, by means of a tube made of caoutchouc, with a second tambour, which bears the registering lever.

Pansphygmograph (of Brondgeest).—This instrument is constructed on precisely the same principles as the preceding ones.

Sphygmograph à miroir (of Czermak).—A small mirror which moves around a horizontal axis receives the transmitted movements of the artery, while a ray of light reflected from the mirror, traces on photographic paper the movements of the instrument, which correspond to the arterial pulsations.

Electric sphygmograph (of Czermak).—To measure exactly the length of the arterial dilatation and contraction, an electric apparatus has been adapted to some of the instruments above described (sphygmometer of Herisson, or sphygmograph of Marey). The opening and closing of the electric current, dependent on the arterial pulsations, enable him to register, with the greatest nicety, the proportional lengths of these phases.

Sphygmograph à gas (of Landois).—The arterial pulsations are transmitted to an apparatus containing gas, a small quantity of which is in this way forced out by each pulsation. The gas is ignited on escaping, and the variations of the flame correspond to those of the pulse. This method of examination has also been employed by Klemensowicz.

Sphygmophone (of Stein).—In this instrument, each elevation of the lever brings a spring into contact with a screw, thereby closing the electric current; a telephone connected with the apparatus allows the openings and closings of the current to be clearly heard. This instrument has been simplified by Dumont.

Microphonic stethoscope.—In this instrument the vertical rod which receives the transmitted pulsations of the vessel, touches at each elevation the carbon-plate of a microphone. By the aid of the telephone, then, a distinct sound is heard, corresponding to the pulsation of the artery, and also to the dirotic wave. It is on this principle that Ladendorff has constructed the instrument so named.

Other methods of investigating the circulation have been adopted, of which the following are the most important:—

Hamautographic method of Landois.—He directs on the paper of the registering apparatus, the stream of blood from an artery, in the coats of which a puncture has been made. The tracings so given by the circulating blood itself are nearly identical with those obtained by the sphygmograph of Marey.

Photographic method.—Czermak so arranges as to let a ray of light fall on the radial artery at the point of pulsation, and receives the reflected rays on

a screen, covered with sensitive paper. Between the point of pulsation and the photographic screen is found a second screen, pierced by a vertical slit, which makes the luminous rays describe vertical lines only on the sensitive paper. Each line is more or less shortened, according to the state of dilatation of the artery, the elevation of the skin by the pulsating vessel intercepting a portion of the luminous rays. Ozanam has devised a similar method, but employs an oscillating column of mercury, as used in the electric sphygmograph of Czermak.

Volumetric sphygmography.—Within the last few years several methods have been devised, for the purpose of measuring the amount of expansion of a limb during the arterial diastole. (1). *Piegu's method.*—A limb (leg or hand) is enclosed in a vessel, which is closed hermetically all around it. It is filled with tepid water, part of which rises into a vertical tube adapted to it, and the oscillations of which are found to correspond to those of the heart, and also to the respiratory movements. (2). This apparatus has been improved in some of its details by Chelius. (3). *Fick's.*—Fick replaces the vertical tube by a V-shaped one, and places in the free branch a small floater, provided with an inscribing lever, as in the kymograph of Ludwig. This enables him to register the variations of volume of the limb. (4). *Plethysmograph of Mosso.*—This apparatus is formed of a glass cylinder, in which the hand and fore-arm is enclosed; a thick caoutchouc band encircles the limb near the elbow, and at the same time hermetically closes the glass cylinder. From the other extremity of the cylinder passes a horizontal tube, which is there bent to a right angle, and passed into a glass vessel. The latter is balanced by a small weight, to which it is attached with the intervention of a pulley. The eprouvette dips into alcoholised water each time that the volume of the imprisoned limb increases; it emerges when the latter diminishes, and the double movement of elevation and depression is transmitted to a balancing weight, to which a pen is attached. (5). *Francois-Franck's.* In this method the limb is enclosed in a cylindrical glass vessel, being introduced through an opening in a caoutchouc membrane, which is supported by a thick disc, formed of gutta-percha. A vertical tube brings the apparatus into communication with a *tambour à levier*, and on this tube is an ampulla, the presence of which prevents the registering of slight oscillations not due to real movements. (6). *Hydro-sphygmograph of Mosso.*—This instrument is related to the apparatus of Francois-Franck just described, and also to the plethysmograph. To the glass cylinder is added a vertical tube which is connected at the other end with a registering *tambour*; the horizontal tube ends in a flask, and is intended to prevent the transmission of very slight oscillations to the vertical tube (*appareil de compensation*).

Pulsatile Vibrations of the Body.—It was remarked by Hartshorn and Gordon, that when a person was placed on a balance, the lever presented oscillating movements synchronous with the pulse, and Hartshorn designed an instrument (*ballograph*) for their registration, which, however, was never constructed. Landois has described and figured an instrument, which registers these vibrations with facility (*Lehrbuch der Physiologie*, 1879), and the tracings so obtained, present a striking analogy to those of the pulse. Contrary, however, to Gordon's observations, the tracings obtained by Landois show, that the whole body at the time of the ventricular systole, suffers a well-marked downward impulse.

Flow in the Arteries.—When the blood is expelled from the left ventricle, under the influence of the *vis a tergo*, which must be sufficient to overcome the intra-vascular pressure in the already over-filled aorta, two results follow: (1). propulsion of the contained column of blood in the direction of the capillaries; (2). dilatation of the calibre of the aorta, till the elastic resistance of its coats comes to equal the blood-pressure. When the ventricular systole ceases, the pressure within the aorta diminishes, and the elastic force of the walls of the vessel, obtaining the mastery, reacts on the contents, and forces the blood partly backwards towards the aortic valve, but chiefly forwards towards the capillaries. The reflux is abruptly stopped by the opposition of the aortic valves, for as a quantity of blood in the sinuses of Valsalva separates their arterial surfaces from the aortic wall, the force of the aortic recoil immediately acts on these surfaces, and forces them down with instantaneous rapidity. The presence of the flexible lunulæ and the corpora Arantii, ensure the hermetic closure of the orifice. There is no opposition from below, as the cessation of the ventricular systole reduces the pressure within its cavity to zero. Accordingly the entire column of blood is propelled towards the periphery, and the head-wave, transmitted along the vessels with great rapidity, dilates them as it goes. This undulatory movement passes along the trunk and branches of the arterial tree at the rate of (in round numbers) 30 feet per second (9.24 metres). This transmitted wave (*forma materiae progrediens*) must not be confounded with the progressive movement of the column of blood itself (*materia progrediens*), of which the rate is ever so much less, as we shall see. "The pulse-wave travels over the moving blood, somewhat as a rapidly moving natural wave travels along a sluggishly flowing river" (Foster).

The dilating head-wave diminishes in rapidity, from the centre towards the periphery; but on the other hand, it is relatively greater in thick-walled vessels, which offer greater resistance; it is more rapid in the lower limbs than in the upper (Weber and Czermak).

Pulse.—The dilatation of the artery (*arterial diastole*), produced by the expansion-wave above referred to, is the cause of the familiar phenomenon of the pulse. The pulse rapidly follows the ventricular systole, the interval corresponding to the short time necessary for the transmission of the undulatory movement which travels, as we have seen, with considerable velocity.

During the pulsation: (1.) the artery expands in both its diameter, longitudinal and transverse. The elongation of the artery becomes permanent in cases of prolonged high tension (cardiac hypertrophy, &c.), giving rise to the appearance of tortuosity observed in such condition. The increase in the calibre of the vessel may be shown by encircling the artery with a flexible tube filled with water, and surmounted by a graduated vertical tube; the oscillations of the fluid indicate the arterial diastole. (2.) The blood-pressure is increased within the artery, causing the sensation of hardness and resistance communicated to the finger, when applied to the vessel. (3.) The velocity of the current is increased.

According to the observations of Czermak, the interval between the systole of the left ventricle and the succeeding arterial diastole (causing the pulse) would be, for the following arteries:—

Common carotid	...	...	0.087 seconds.
Radial	...	...	0.159 "
Dorsalis pedis	...	...	0.193 "

An examination of a pulse tracing (Fig. 20), obtained by means of Marey's sphygmograph, offers the following points for consideration:—

(1) The lengths of the individual pulsations are generally equal, and, of course, in inverse ratio to the number of pulsations in any given unit of time. The normal number per minute varies from 65 to 75; when less, the pulse is said to be infrequent

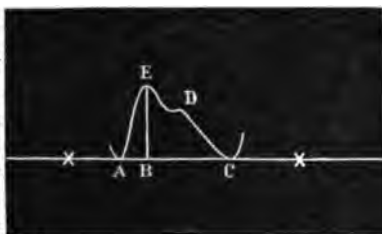


Fig. 20.

(*pulsus rarus*), when greater, it is frequent (*pulsus frequens*).

(2) In the normal state there is no interval of arterial repose; the systole and diastole succeed without interruption, and the angles between the lines of ascent and descent are always acute.

(3) The proportion of the diastole to the systole is about 1:3. *Quickness* and *slowness* of pulse depend on the ratio of these periods; if the duration of the diastole is short the pulse is said to be *quick*; when the duration is above the average, it is said to be *slow*.

(4) The *line of ascent* (A E) approaches the vertical ; it is nearly a right line. This indicates that the arterial diastole is *uninterrupted*, and of almost *instantaneous* rapidity.

(5) The *line of descent* (E C) presents a very considerable obliquity, and instead of forming a continuous straight line, it presents, before reaching the base line, one or more elevations and notches, more or less pronounced (*dicrotism* or *polycrotism*) of pulse).

(6) The *amplitude* of the pulsation, measured by the elevation of the summit of the tracing above the base line, is usually in inverse ratio to the pressure within the artery. The terms *hard* and *soft* applied to the pulse denote, respectively, high and low pressure of the column of blood, and the corresponding state of arterial tension dependent thereon.

(7) The pulse is full or small according to the increase of the volume of the artery during its diastole, a condition varying with the quantity of blood expelled by the ventricle.

We see, by analysing these variations, that the characters of an arterial pulsation vary according to the conditions of three factors : (1) the force of the heart ; (2) quantity and pressure of blood ; (3) condition of the arterial wall (elasticity and contractility).

The interpretation of the tracing obtained by the sphygmograph has given rise to a great deal of discussion. The line of ascent and the summit, corresponding (as explained above) to the expansion wave produced by the ventricular systole, present no difficulty. But the *secondary waves* which interrupt the line of descent are more troublesome to deal with. Vierordt attributed them altogether to mechanical imperfections in Marey's instrument, as they did not appear in his own tracings ; but they are now universally regarded as a normal feature. That they are not due to oscillations of the lever has been conclusively proved by the *hamautographic method*, already described, in which the curve is formed by a jet of blood coming from an opening in the artery, and without the intervention of any apparatus. The *dicrotic wave* (D) is better marked in the smaller arteries than in the great trunks. The interval between the primary and dicrotic waves becomes longer as we recede from the heart, and the wave summit is less pointed. The dicrotic wave diminishes as the arterial tension increases. In the normal condition it cannot be felt by the

finger; but in cases where the arterial tension falls very low (typhoid fever, advanced hectic, &c.) it becomes quite distinct, and each pulsation conveys a double stroke to the finger. It has been supposed to be a wave of reflection from the periphery, produced by the capillary resistance, or reflected from the angles of bifurcation of the arteries, or from the corpuscles entangled in the capillaries (Onimus and Viry). It has been supposed to be due to the wave produced by the second reflection from the semilunar valves of the wave which had been first reflected back from the periphery (Rive). Another idea is, that it is due to the rebound of the column of blood from the aortic valves when the latter have been forcibly shut down by the elastic recoil of the coats of the aorta (Landois, Galabin). Marey attributes it to oscillation of the wall of the arterial tube. Moens points out that whenever there is an intermittent flow of blood into an open elastic tube, there are developed what he calls secondary waves of closure (*ondes secondaires de fermeture*). When the aortic valves are shut down, the column of blood, under the influence of the acquired increase of velocity, and the elastic pressure of the aortic wall, continues to move towards the periphery, the aortic canal narrows beyond the normal limits, but soon tends to reassume its normal dimensions, and, in expanding, causes the reflux of a certain quantity of blood, which dilates it. A secondary wave is thus developed, which travels from the origin of the aorta onwards, distending the arteries in its course. Burdon-Sanderson explains its formation by the secondary distension of the vessel produced by the elastic recoil of the walls of the vessels in front of the point examined. Foster looks upon it as a result of the combination of two factors; being partly produced by the new wave of expansion which starts from the closed semilunar valves, and partly by a wave of oscillation developed in the wall of the vessel.

A *predicrotic wave* is sometimes seen to precede the wave of true diastole. It is believed by most authorities to be merely a wave of oscillation. If very well marked, the pulse is said to be *tricrotic*. Sometimes a small elevation is found on the line of ascent, before the summit is reached; the pulse which presents this peculiarity is said to be *anacrotic*, the more normal one being said, in contradistinction, to be *catacrotic*.

Frequency of the pulse.—The normal rate of the human pulse

or heart beat is about 72 per minute (65—75). (*Influence of age.*) It is much quicker in foetal life, and diminishes in frequency up to maturity. The rate increases a little again in old age. (*Sex.*) It is more frequent in the female than in the male. (*Stature.*) It is also more frequent in people of short stature (Volkman, Rameaux). (*Exercise.*) The rate is increased by exertion, and it is accordingly greater in the standing than in the sitting posture, and greater when sitting than in the horizontal position. (*Time of day.*) The rate of the pulse also diminishes from morning to noon, and increases again from noon to evening. (*Season.*) It is quicker in summer than in winter. It is also increased by *ingestion of food*, elevation of *temperature*, and *mental excitement*. Mental depression is accompanied by a diminution in the rate of frequency. Ascent to a *high altitude* is accompanied by great quickening of the pulse, independently of muscular exertion.

Form of the pulse.—*Heat* increases the amplitude as well as the frequency of the pulse, the dicrotic wave also becoming better marked. The *time of day* has also a considerable influence. In the morning the line of ascent is less vertical, and the summit is more rounded; it soon becomes rapid, dicrotous, and more ample. The same effect is produced by *muscular exercise*. The influence of *mental exercise* is also very striking; the amplitude of the tracing diminishes, the dicrotic wave is more pronounced, the predicrotic wave is also better marked and situated nearer to the summit than it usually is; the latter is more elevated above the base line. With these changes there is also a marked increase of frequency. *Attitude* also affects the form of the pulse. In the horizontal position, the summit is more rounded, while the amplitude is diminished. When the *arm is elevated* the amplitude of the curve increases, and the dicrotic wave becomes more marked; when *depressed*, the amplitude diminishes, and the dicrotic wave disappears. *Compression of a large artery*, such as the femoral, produces a similar result, by increasing the arterial tension. *Digestion* increases the amplitude as well as the frequency of the arterial pulsations; both dicrotic and predicrotic waves become better marked. *Pressure* on an artery modifies the character of the tracings obtained; when slight, the curve is still elevated, and dicrotism fairly well marked; as the pressure is increased the amplitude of the tracing diminishes, and dicrotism becomes

less marked; later on, the predicrotic wave becomes more pronounced, and the descending part of the curve becomes longer and more oblique. *Increased frequency* is generally accompanied by a diminution of amplitude, the diminution being at the expense of the part of the line of descent below the dicrotic wave; the next change is the disappearance of the dicrotic wave. *Increase of the blood pressure* diminishes the fulness of the curve, while the general level is elevated. The dicrotic wave disappears, but the predicrotic wave becomes more pronounced (Landois).

The *influence of respiration* on the form of the pulse differs according as we study the former in the normal or the laboured form. In calm superficial respiration no difference is observed between the tracings of inspiration and those of expiration. If the expiratory movements be more ample and the air-passages completely free (mouth and nose open), the general level of the tracings is raised during inspiration, and depressed during expiration; the reverse is the case if marked obstruction exists (as by shutting the mouth and compressing one nostril). Also, during expiration the pulse is less frequent, the curve more ample, the dicrotic wave more pronounced, and the predicrotic and oscillatory waves less so than during the inspiratory movement. During *violent effort*, or in *Valsalva's experiment* of making a forced expiration with the mouth and nose closed, the general level of the pulse-tracing is elevated, and it presents all the characters of high tension; if the effort continue, the tension gradually diminishes, and the dicrotic wave reappears; then, on the cessation of the effort, the general level sinks rapidly, and the characteristics of tension disappear the pulsations are scarcely discernible at first, but gradually return to the normal form. If a deep inspiratory movement be made with the mouth and nose closed (*Müller's experiment*) the pulse shows evidences of diminished tension, and the dicrotic wave is better marked, but the results are not so well pronounced as in the other case.

In certain pathological conditions the pulse becomes very small during inspiration, and may even disappear altogether (*pulsus paradoxus*).

Contradictility of Arteries.—This property is proportionally better marked in the smaller arteries on account of the predominance of the muscular element in their walls. It is under

the influence of the nervous system, and completely independent of the heart's action.

It manifests itself in one of two ways: it may last for some time, causing a diminution of the calibre of the vessel of some duration; or it may be intermittent, presenting the phenomenon of alternate contraction and relaxation. These successive contractions are often rhythmic; they are seen on the small arteries only, and are not isochronous with either pulse or respiration. Their rate of frequency is very variable, but generally low compared with that of the pulse (3—7 per minute). These movements have been studied by Schiff in the ear of the rabbit, and they have been observed in the iris, mesentery, and other tissues. The cause is very obscure; the function, doubtless, is to regulate the quantity of blood passing through a given capillary area. The intervening dilations are probably due to the yielding of the walls of the vessel, during the period of relaxation, to the pressure of the contained column of blood. Schiff looks upon it as an active movement due to the influence of vaso-dilator nerve fibres.

The influence of the persistent form of contraction on the corresponding capillary area is, of course, more marked, and when it engages a considerable vascular tract the effects make themselves evident over the entire remaining part of the vascular system, causing an increase of the quantity of blood going to other parts, to neighboring organs especially. Examples of this *balance of local circulations* are found in many parts; it is found in the relation between the thyroid and cerebral circulation, between the gastro-hepatic and splenic, and on a large scale between the cutaneous circulation and that in the deeper parts; between that of the head and of the upper limbs; between the abdominal circulation and that of the lower extremities.

We shall make some further remarks on the subject when we come to examine the influence of the nervous system on the circulation.

CAPILLARY CIRCULATION.

To study the capillary circulation a translucent membrane is generally chosen, such as the web of the frog's foot, or the mesentery of the same animal. The frog is first brought under the influence of curara, to prevent disturbing movements. The tongue of the animal also furnishes a good object for microscopic examination. Holmgren has devised an

apparatus by which the capillary circulation of the lung may be examined. A canula is introduced into the trachea for the purpose of distending the lung, and the escape of the air is prevented by a stopper. A compressing instrument then flattens a piece of the lung, whilst it at the same time diminishes the capillary circulation, thereby rendering it more transparent. The tail of the tadpole, and young embryos of various animals, especially of fishes, also furnish favourable objects for the study of capillary circulation. In warm-blooded animals greater difficulty is experienced, but the mesentery of small animals can be manipulated with moderate ease. The *membrana nictitans* of the pigeon, and the corresponding structure in the rabbit, have also been studied.

Under the name of *cheilo-angiostomy*, Hunter has described a mode of procedure devised by him for the study of the capillary circulation in the human being. He draws forward the everted lower lip, and having fixed it with the aid of small forceps, he examines the capillaries with a magnifying power of 53 degrees.

The arrangement of the capillaries varies according to the tissue examined. They usually form a dense *polygonal* meshwork, as throughout the tissue of the cutis vera, in the mucous membranes, the lungs, and the various glands. In tissues formed of parallel fibres, as in voluntary muscles, in tendon, and in nerves, the capillary network forms *elongated* meshes, the long axes of the spaces running parallel to the constituent fibres.

The *vascularity* of a part is determined by the size and arrangement of its capillaries. In the lungs which are intensely vascular the diameter of the capillaries is much greater than the breadth of the intervening spaces. Similarly in the choroid coat of the eye. In the liver the diameter of the spaces is about equal to that of the capillaries. In the brain the long diameter of the meshwork is about ten times that of the capillaries, the transverse diameter being about four or six (Weber).

In examining the capillary circulation, we find that the blood current is continuous and uniform, and does not present the intermittent accelerations of velocity presented by the arterial flow. If the capillary vessel be a large one we find that the layer in contact with the wall of the vessel appears almost immobile (*inert layer*), while the axial part of the fluid moves with comparative rapidity. The pale corpuscles are found in the inert layer, clinging to the wall of the vessel, and often stopping entirely, while the red are found in the axial current, progressing at a rate of ten to fifteen times that of the pale. It is necessary to remember in making these observations that under the magnifying power the rate of the current

appears greater than it really is, in proportion to the microscopic power employed. In the smallest capillaries a single corpuscle can barely squeeze through by altering its shape.

The capillaries are subject to *variations of calibre* which are of two varieties. One is *passive*, and due to the varying degree of pressure in the interior; the other is *active*, and due to the contractility of the capillary wall (Stricker). This contractility may be thrown into action by electric stimulation, and also by chemical and mechanical irritants, as in case of muscular fibre. The endothelial cells of the capillary wall become shorter and thicker, and so produce the contraction (Jarchanoff). If the mechanical irritation be too violent, dilatation follows instead of contraction (Marey). According to Bloch, every mechanical irritation, however slight, is followed by dilatation.

A *derivative circulation* has been described by Suquet in the fingers, scalp, &c., formed by branches passing directly from the arteries to the veins, and independent of the capillaries.

Diapedesis.—By this term is understood the passage of blood-corpuscles through the capillary walls. That this process of migration was continually going on was not generally known till the publication of Professor Cohnheim's observations on the subject in 1867, although it had been noticed more than twenty years before by Dr. Addison and Dr. Waller. If the capillary wall be closely watched under the microscope a leucocyte is seen to pass through from time to time, first projecting on the outside as a button-shaped elevation, then as a pear-shaped body, attached by "a slender thread, by which it is still moored to the vessel." This thread soon breaks off, and the separation is complete. The subsequent fate of the emigrant leucocyte in its wanderings through the connective-tissue spaces is not definitely known.

The diapedesis of *red* blood-corpuscles was first described by Professor Stricker, but is seldom seen.

VENOUS CIRCULATION.

The flow in the veins is uniform and continuous. It is determined, as is the course of the blood-current elsewhere throughout the area vasculosa, by the direction of diminished pressure; and although the venous system forms a cone, the apex of which is at the heart, and the base at the capillaries, and in which the pressure should accordingly increase in the

direction of diminution of sectional area, yet the increase of pressure is more than compensated for by the regular periodic emptying of the auricle, and the result is a total decrease in the direction of the heart. The venous current is promoted by the contraction of the surrounding muscles, when this does not go so far as to obliterate the vessel completely. It is also favored by the numerous anastomoses between neighboring veins, the pulsations of the corresponding arteries, by gravity in some veins, and most of all by inspiration.

It is only in pathological conditions that we have a *venous pulse* synchronous with the auricular systole.

PRESSURE OF THE BLOOD WITHIN THE VESSELS.

MODES OF EXAMINATION. (A) Simple Manometer.—This method was used by Hales, who adapted a long, straight tube to an opening in the wall of a vessel of corresponding size, and then watched the height to which the blood rose within it.

(B) Mercurial Manometer.—*Hæmadynamometer* (Poiseuille). In using this instrument the horizontal limb of a bent glass tube was introduced into the open end of a divided vessel. The greater part of the length of the vertical limbs was filled with mercury, and the interval was filled with an alkaline fluid which prevented coagulation. The pressure of the column of blood forces down the mercury on that side, which then rises to a corresponding height on the opposite, and the difference between the points of level represents the column of mercury which the blood can sustain under the influence of the pressure transmitted from the heart.

Hæmometer (Magendie) or *Cardiometer* (C. Bernard). In this instrument the lower part of the tube is replaced by a large basin filled with mercury. This communicates on one side with a tube filled with an alkaline solution, which is introduced into the vessel, and on the other with a vertical tube in which the mercury oscillates. The variations in the mercurial column are much more sensible than in the preceding instrument.

Differential Manometer (C. Bernard).—This instrument is formed of a bent tube of which each of the two parallel branches communicates with flexible tubes and cannulæ; the two cannulæ are then introduced into separate vessels, and the difference of level of the two columns of mercury represents the difference of pressure within the two vessels examined.

Compensatory Manometer (Marey).—Marey has pointed out two great

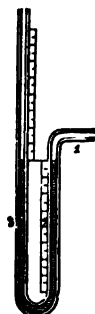


Fig. 20.
Hæmadynamometer.

1. End introduced into open artery.
- 2, 3. Bent portion containing mercury.

sources of fallacy in the observations recorded by the ordinary manometers: (1) The oscillations of the mercurial column are too great on account of the acquired velocity of the liquid mass; (2) the ascent of the mercurial column is more rapid than its descent, so that the mercurial mean between the maximum and minimum points of elevation does not really represent the medium blood-pressure (*tension dynamique*). He accordingly endeavors to obviate these drawbacks by interposing between the vessel containing the mercury and the vertical tube, a capillary tube, which, by its resistance, diminishes the amplitude of the oscillations, and gives the mean pressure as nearly as possible. Setschenow substitutes for the capillary tube a stop-cock, which he opens more or less fully.

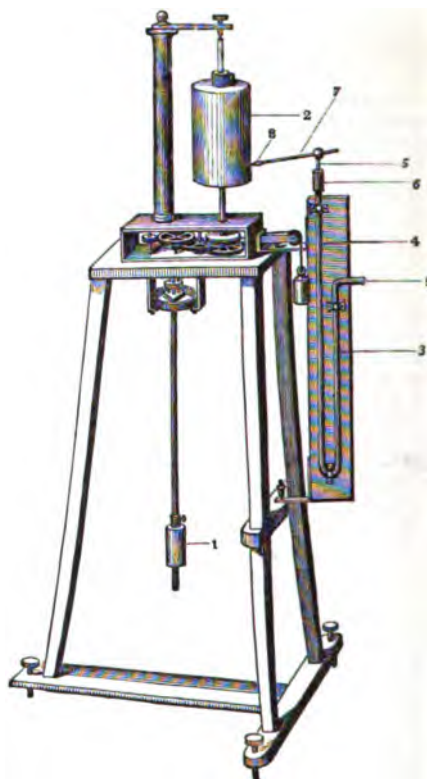


Fig. 21. LUDWIG'S KYMOGRAPH.

Kymograph (Ludwig).—This is simply a hæmadynamometer to which is attached a registering apparatus. One limb of the apparatus (3) is curved (Fig. 21), and made to communicate with the artery (at 9). On the upper surface of the column of mercury in the other branch (4) is floated an ivory cylinder, surmounted by a stem (5), to the upper end of which is attached a brush or pencil (7, 8), which traces the oscillations of the column of mercury on the cylinder (2) of a registering apparatus. The latter is made to revolve by the traction of a weight (1) suspended vertically.

Manometer of François (*manomètre à mercure inscripteur modifié*). In this instrument the short limb of the U-tube is provided with a spherical reservoir. This has the mechanical effect of making the change of level of the mercury in the long limb to correspond to the full value of the changes of pressure instead of half, as in the manometer already described. There are slight modifications also in the registering apparatus. François-Franck has constructed on the same model a double manometer which allows the simultaneous registration of the blood-pressure in two vessels.

(c) **Metallic Manometers.** *Fick's Kymograph.*—Fick has constructed an instrument on the principle of Bourdon's barometer. It consists essentially of a hollow metallic spring, of which one extremity is fixed, and communicates by means of a flexible tube with the cannula which has been inserted into the divided vessel; the other end is moveable, and connected by a system of jointed levers, with a registering apparatus which traces, in magnified form, the movements of the free end of the spring.

Recording Manometer (Marey's).—In the interior of a flattened metallic vessel is placed a capsule of an aneroid barometer filled with fluid, and opening externally by a tube which passes through the wall of the enveloping vessel; that tube terminates in a flask, to the neck of which is connected a flexible tube furnished with a stop-cock. In the top of the investing vessel is an opening, through which passes a glass tube into which water is poured, so as to fill the vessel, and the tube itself to half its height. The level of this layer of fluid then rises or falls with the pressure in the capsule. To register the oscillations of the liquid, a caoutchouc tube is adapted to the glass tube, and connecting with a recording tambour.

Manometer à cadran (Tatin).—In this instrument the absolute values of the pressures are indicated by a needle on a dial previously divided by testing with a mercurial manometer.

(d) **Elastic Non-metallic Manometers.**—Under this heading may be classed the *sphygmoscope* of Marey. It is formed of an ampulla of indiarubber placed within a glass cylinder, and the interior of the ampulla communicates by a tube with the artery, the pressure of which is to be ascertained. The variations of pressure are transmitted to the ampulla, and cause vibrations of the air within the glass cylinder, which are transmitted to the atmosphere, and by means of a tube to the tambour of the polygraph.

Pressure of Blood within the Capillaries.—For the purpose of ascertaining the pressure of blood within the capillaries several methods have been devised. Small square pieces of glass, furnished with weights, have been applied to the skin till the paleness of the latter showed that the blood had been expelled (V. Kries). Another procedure adopted by Roy and Graham is that of observing with the microscope the capillary

circulation in a transparent membrane whilst the latter is submitted to graduated pressure.

Besides the method of Kries, mentioned above, other plans have been used for the purpose of ascertaining the pressure within the blood-vessels of the human body. Marey enclosed a limb (fore-arm, or finger) in a glass cylinder, and around it an encircling band of india-rubber renders the open end of the vessel air-tight. The latter is filled with water, and the vibrations produced by the varying distention of the blood-vessels of the limb are transmitted by a connecting tube to a registering manometer (Fig. 22).



Fig. 22.

In general terms it may be said that the blood-pressure diminishes from the heart to the capillaries and from the capillaries to the heart; the point of maximum pressure is in the ventricle during systole, while the minimum is that of the auricle during diastole. In the latter, and in the great veins, it may fall below the atmospheric pressure during diastole. Poiseuille, on account of the imperfection of the apparatus which he employed, was led to believe that the pressure was equal along the whole arterial system.

In the carotid of man the mean pressure has been estimated at 160 mm. of mercury; in that of the horse at 280; of the dog 150; of the rabbit 50-90. This pressure keeps the arteries in a state of *permanent distension*. The arterial pressure is subjected to two opposing forces: (1) the propelling force of the heart, which urges the blood onwards with intermitting activity; (2) the retarding influence of the small vessels which, by their contractions, prevent the easy escape of the blood from the arteries into the veins.

The influence of the arterial pressure on the rate of the heart's action has been disputed, but Marey has proved that if the nervous influences, &c., be equal, *the frequency of the pulse is in inverse ratio to the arterial pressure*. His experi-

ment is that of taking the heart of a turtle from the body, and, while continuing to beat, he connects it with a system of tubes containing fluid which is kept moving by the contractions of the heart; when the resistance is increased by compression of the tubes, the number of pulsations diminishes.

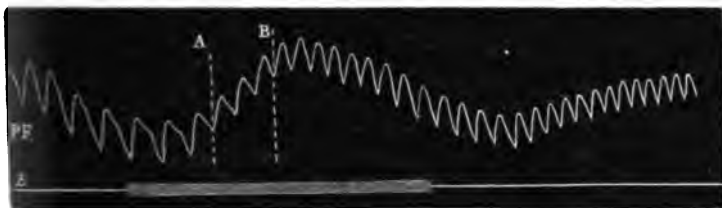


Fig. 23.

TRACING OF BLOOD-PRESSURE IN FEMORAL ARTERY OF DOG (Marey).

The means at our disposal for estimating the *pressure in the capillaries* can give, at best, but approximate results. It must be intermediate between the arterial and the venous pressure, and determines the transudation of plasma through the capillary walls, and the various changes that take place between the blood and the tissues. V. Kries has given 37.7 mm. of mercury as the representative of the capillary pressure in the last phalanx of the human digit.

The *venous pressure* is much less constant than the arterial. It has been found that the pressure in the great veins near the heart is usually from a tenth to a twentieth of that within the corresponding arteries, while during the auricular diastole it may fall below zero.

Cardiac pressure.—The pressure in the various cavities of the heart presents the widest range of variation. Chauveau and Marey found the pressure in the left ventricle of the horse to be 128 mm.; in the right ventricle, 25; in the right auricle, 2.5. The pressure in the pulmonary system is much less than in the general circulation. Ludwig has found that in the pulmonary artery to be 10-30 mm. of mercury.

We have already seen that the quantity of blood is very considerably in excess of the natural capacity of the vascular system, in consequence of which the walls of the vessels are kept in a state of permanent tension. This is necessary for the maintenance of a *continuous* current through the capillaries, and for the transudation of the liquor sanguinis through the

walls of the latter, on which depend the various nutritive changes which are essential for the maintenance of the phenomena of life. An attempt has been made to ascertain the mean tension of the area vasculosa by stopping the heart's action by stimulation of the pneumogastric; the pressure then falls in the arteries and ascends in the veins, till a general equilibrium is established, representing a pressure of 10 mm. of mercury (Brunner, Einbrodt).

Velocity of the Blood Current.

The velocity of the blood diminishes from the heart towards the capillaries, and increases from the capillaries along the veins towards the heart. Various forms of apparatus have been devised for the purpose of ascertaining it; the results, of course, cannot be taken as very accurate, the sources of fallacy being so numerous, but they are, at least, approximately true.

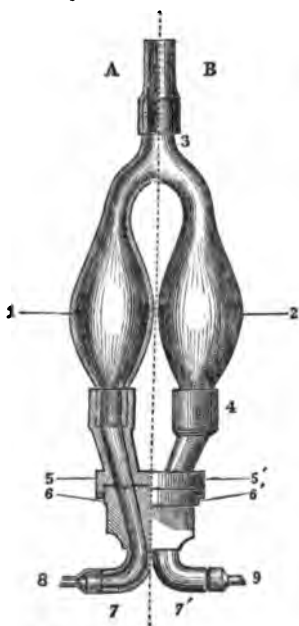


Fig. 24.

Hæmodromometer (Volkman's).—This instrument consists of a short metallic tube, connected to which is a U-shaped glass tube, filled with a colorless alkaline solution. By the action of the two stop-cocks the communication of the straight tube may be cut off completely from the U-tube, so that fluid admitted at one end of the straight tube passes directly through; by turning the cocks, the fluid flows along the U-tube. In using this instrument the ends of the straight tube are introduced into the adjacent openings of a divided artery of the corresponding size, and blood is at first allowed to flow along the straight tube. The cocks are then suddenly turned, the flow of the blood along the U-tube is watched, and the time noted. As the length of the tube is known, the velocity is easily calculated.

Stromuhr (of Ludwig and Dogiel).—In this instrument two ampullæ (1, 2), made of glass, and of measured capacity, communicate at one end with a single tube (3) and at the other with two tubes (7, 7'), which are in turn adapted to the open ends of a divided blood vessel by the mouth-pieces (8, 9). The ampullæ are supported on a disc (5, 5'), which revolves on a second disc (6, 6') placed beneath it in such a

way that each ampulla can be made to communicate alternately with the tubes 7 and 7'. Before commencing the operation the ampulla 1 is filled with defibrinated blood, and ampulla 2 with oil. The apparatus is placed in the position indicated in the figure, the tube 7' is placed in communication with the central end of the artery, and the tube 7 with the peripheral extremity. The blood entering 7' forces the oil of the ampulla 2 into ampulla 1, from which the defibrinated blood passes into the peripheral end of the artery. The instant at which the arterial blood enters the apparatus is noticed, also the instant at which it fills the ampulla 2 up to a certain point previously marked. In this way the time is known which the quantity of blood corresponding to the capacity of the ampullæ requires to pass along the artery, and the velocity of the current is then easily calculated. The operation is recommenced by turning the disc 5, 5'; the ampulla 1, filled with oil, then communicates with the central end of the artery through the tube 7', while the ampulla 2, filled with blood, communicates with the peripheral end. In this way it is repeated several times, in order to increase the accuracy of the observations.

Hematochrometer (Vierordt's).—This is a glass vessel with parallel rectangular sides; a tube opens at one end, which admits the blood, and at the opposite side is another, which gives exit to the moving fluid. The latter, in passing through, moves a pendulum which is furnished with a silver ball, from which a thin rod passes on each side to the inside of the glass vessel so as to touch without friction. This enables the observer to make out the position of the pendulum, notwithstanding the opacity of the blood, and its deviation from the perpendicular is marked by a graduated arc. He has completed the instrument by connecting it with a registering apparatus.

Hæmodromograph (of Chauveau and Lortet).—A tube, made of copper, is adapted by both ends to the openings of the divided vessel. On one side is an opening, which has been closed by an accurately-fitting piece of india-rubber membrane. The latter is traversed by a needle, which projects into the tube, and of which the opposite extremity terminates in a writing point, which is placed in contact with the paper of a registering apparatus. The current of blood passing along the tube causes a deviation of the needle. Marey's sphygmoscope has been adapted to it, so as to register separately the variations of the blood pressure within the artery.

The microscope has been employed to measure the flow of blood in the capillaries, by the aid of a micrometer. Vierordt has employed the entopic method for the purpose of determining the velocity of the flow in the retinal capillaries.

To estimate the time occupied by the blood in going the whole round of the circulation, Hering has employed Blake's experiment of injecting a solution of ferrocyanide of potassium. On introducing a small quantity into the external jugular vein on one side, and withdrawing from the opposite vessel a small quantity of blood, at intervals of five seconds, he can tell to a nicety, by testing with a per-salt of iron, how long it took the blood to circulate (through the upper segment

of the body, at least). Vierordt has perfected this method by adapting small vessels, prepared to receive the blood from the open vessel, to the revolving disc of a registering apparatus, and so secures a new specimen of blood every half second.

Whilst the velocity of the blood is constant and uniform in the small arteries, as well as in the capillaries and veins, each ventricular systole causes a great increase of the rate of the current in the large arteries. In the great veins near the heart rhythmic variations in the velocity of the blood take place with respiration. The causes on which the rate of the current depend are : (1) the *energy* of the heart's action (there is no constant relation between the frequency of the beats of the heart and the velocity) ; (2) the *differences of pressure* between the origin and termination of the *area vasculosa* (the *mean* pressure has no influence, and it may be increased or diminished by the injection or withdrawal of blood without changing the rate of the flow) ; (3) the quality of the blood ; certain substances introduced into the vessels (alkalies, &c.) increase its rate (Aronheim) ; (4) obstacles to the course of the current, especially the variations in the calibre of the blood vessels, due to the influence of the nervous system.

PULMONARY CIRCULATION.

The organs of this system are all enclosed within the thoracic cavity, and the pulmonary artery and veins are submitted to the same negative pressure, with the same variations, as that affecting the heart, aorta and caval veins ; but whilst the capillaries of the general circulation are subjected to the almost unchanging atmospheric pressure, the pulmonary capillaries, situated within the thorax, undergo an external pressure, varying according to the respiratory phases. The question of the exact influence of the inspiratory and expiratory movements on the pulmonary circulation has given rise to a great deal of contradictory discussion, and has been studied experimentally by several physiologists (Quincke and Pfeiffer, Funke and Latschenberger, Mosso, &c.), but there have been too many discrepancies in the obtained results to enable us to arrive at any very definite conclusions. The balance of evidence is in favour of the assertion that the inspiratory act promotes the pulmonary circulation, for the lung preserves all its redness

whilst its size increases so much. Expiration retards the pulmonary circulation, and in certain conditions may even completely arrest it. We shall examine the subject more fully.

INFLUENCE OF THE RESPIRATION ON THE CIRCULATION.

The respiratory act has a well-marked influence on the circulating blood, affecting both the pressure and the velocity.

During *inspiration* the diminished intra-thoracic pressure has the effect of lowering the blood-pressure within the cardiac cavities and in the great vessels; this diminution of pressure causes aspiration of the blood towards the great veins and right side of heart, while it retards the current through the left heart and aorta. Accordingly, if the influence exercised on each of the two sets of vessels were the same, the total result on the circulation, as a whole, would be *nil*; but the thinner walls of the veins and of the right cavities of the heart are more easily affected by alterations of pressure than those of the arteries and of the left side. The veins transmit, in this way, an increased quantity of blood to the heart, and when brought to the right side it is at once transmitted to the left and onwards, so that the result of the inspiratory act, upon the whole, is to promote the circulation very considerably, and the fulness and frequency of the pulse is found to be increased. If, however, a very deep inspiration be taken, and the mouth and nose then tightly closed, the intra-thoracic pressure falls very much (50—90 mm.) below the atmospheric pressure, a condition which has the effect of causing engorgement of the cavities of the heart and slowing of the pulse (Donders).

Expiration has an opposite effect; the pressure within the thorax increases, and accordingly the calibre of the great vessels diminishes, the venous circulation is retarded, while the arterial is promoted; the heart receives less blood, and its beats become less frequent and less forcible. By maintaining a powerful expiratory effort with the glottis closed, the heart's action may be brought to a stand-still (Weber).

These observations would seem, on superficial examination, to account for the respiratory undulations in the blood-pressure curve by a simple mechanical influence, but it is found, on more careful study, that many objections present themselves which entirely forbid such a conclusion.

In ordinary respiration the influence on the blood-pressure is but very slight. The researches of Einbrodt and Burdon-Sanderson have shown that, contrary to the results of Ludwig and his school, the arterial pressure (carotid, femoral, &c.) increases during inspiration and diminishes during expiration. The respiratory variations precede, by a minute period, those of the arterial pressure. In the dog the pulse-rate is quickened during the rise of the pressure-curve; slowed during its fall (see Fig. 23). In the rabbit, while the undulations are well marked, rate is hardly affected. In an animal poisoned by urari, the pulse-undulations of the blood-pressure curve, obtained while artificial respiration is maintained, are similar to the ordinary curves, although not quite so well pronounced. This latter fact is quite sufficient to disprove the idea that the variations in the pressure-curves were due to the mechanical effects of the inspiratory movements, for when the lungs are artificially inflated through the trachea, the intra-thoracic pressure is increased instead of being diminished. Another explanation that has been offered is, that the entrance of air, by distending the pulmonary alveoli, stretches the capillaries in their walls, and so, by narrowing the calibre of the latter, has the effect of retarding the passage of blood through the lungs. This probably would hold good only for artificial respiration; during normal inspiration the diminished pressure on the exterior of the lungs would tend to widen the capillaries in the alveolar walls. In this case, nervous influence has probably more to do with the undulations in the pressure-curve.

In the dog the difference in the pulse-rate during expiration and inspiration is at once done away with by section of the pneumogastric nerves, so that the slowness of pulse observed during the fall of the curve-line is evidently due to stimulation of the cardio-inhibitory centre. After poisoning by urari, when the artificial respiration is stopped, the respiratory undulations cease also, and a great increase of pressure takes place, so that the curve rises almost in a straight line. In a short time new undulations appear, somewhat similar to the natural ones, but larger and more sweeping in outline (*Traube's curves*). These curves are present even when the vagi have been divided, but they are greatly diminished by section of the spinal cord. They are evidently dependent on the vaso-motor centre, as they are present without either thoracic or pulmonary movements.

They continue during the rise of the blood-pressure and disappear with the fall of the latter, when both heart and vaso-motor centre become exhausted by the increasing venosity of the blood.

For the proper maintenance of the circulation in the various organs of the living body, means of adaptation are necessary, by which a greater or less quantity of the vital fluid is supplied according to the conditions of rest, activity, &c. The chief modifying agencies are :—

- (1) Changes in the force and frequency of the heart's action.
- (2) Changes in the peripheral resistance, due to variations in the calibre of the small arteries, produced by contraction of the muscular coats.
- (3) Changes in the permeability of the capillary walls.

Influence of the Nervous System on the Circulation.—The heart of a cold-blooded animal will continue to beat for hours or even days after its removal from the body, and even after the cavities have been emptied of blood. The action is more vigorous if the sinus venosus have been left attached. If a part or the whole of the auricles be left behind with the sinus venosus in the body, this part goes on beating by itself while the ventricular segment pulsates, although not so vigorously. If the auricle be cut into several pieces each piece still contracts by itself; if the ventricle be divided longitudinally the lateral portions continue to pulsate, but if the incision be transverse, the basic segment still contracts, while the lower portion remains motionless. Careful examination of the cardiac wall has shown that in the parts possessed of spontaneous pulsation ganglia are present, and as they are absent elsewhere, the conclusion arrived at has been that the movement is due to the influence of these ganglia. The position of three of these ganglia has been ascertained: (1) the *ganglion of Remak*, at the opening of the inferior vena cava; (2) the *ganglion of Bidder*, in the left auriculo-ventricular septum; (3) the *ganglion of Ludwig*, in the interauricular septum. Of these the first two appear to have an exciting influence, whilst the function of Ludwig's ganglion seems to be inhibitory. If the heart be cut into two unequal segments, so that one encloses the ganglion of Remak, and the other the ganglia of

Bidder and Ludwig; the former piece continues to pulsate, whilst the latter remains motionless. If the auricles be then separated from the ventricle, the latter commences to contract whilst the former segment remains still. The intermediate ganglion of Ludwig then evidently has an inhibitory influence on the action of the others; being a match for a single one, it is able to paralyse it when opposed by it alone, but in the living heart it is unable to do more than to moderate the action of the other two.

The lower part of the ventricle, when lying immobile after separation from the rest of the heart, may be thrown into rhythmic contraction, like that of the normal beat, by the application of the constant current. A single induction shock causes a single contraction, and it is a remarkable fact that there is no relation between the strength of the stimulus employed, and the force of the resulting contraction. When a second induction shock is sent in at a certain interval from the first, the resulting beat is often more powerful than the other, but if the second shock is applied too soon there is no result. The application of the ordinary interrupted current causes a rhythmic succession of beats; tetanus cannot be produced.

Inhibition of the Heart's Action.—Stimulation of one of the vagi nerves produces, when the stimulus is but slight, a slowing of the action by prolonging the diastole. When the stimulus is sufficiently powerful, the contractions entirely cease. This fact was discovered by E. Weber (1845). The latent period in the application of this inhibitory action of the vagus is long; .16 seconds in the rabbit (Donders). This inhibitory action of the pneumogastric nerve is soon exhausted, its maximum is observed soon after the commencement of the stimulation, and if the stimulus be long maintained, the action of the heart recommences before removal. During the period of inhibition direct stimulation, as by touching, is followed by a single contraction, showing that the irritability of the muscular fibres has not been affected. The right vagus influences the heart more than the left (Maison, Arloing, Tripier). The arrest produced in the dog by vagus stimulation lasts from fifteen to thirty seconds. Section of the spinal cord and of the two sympathetics in the neck increases the inhibitory influence of the pneumogastric, so that a very slight irritation is enough to arrest the heart's action. If the sinus venosus be separated

from the auricles by an incision carried along the boundary-line between them, the contractions are arrested for an indefinite period, but during the time of rest a series of contractions may be produced by the application of a mechanical stimulus over the situation of Bidder's ganglion, or to the ganglia in the auricles and in the bulbus. The ventricles, if removed by an incision from the auricles, will be found to recommence beating, whilst the auricles still remain at rest. The application of the constant current produces rhythmic contractions, characterised by a tendency for the ventricular systole to appear before that of the auricles.

Reflex irritation also determines the inhibitory action of the pneumogastric nerves. This is shown by stimulation of the mesenteric branches of the sympathetic, or even by sharply striking the intestine or peritoneum of an animal after the abdomen has been laid open. Intense pain causes stoppage of the heart's action, as may be seen by the experiment of crushing a frog's foot. Section of the pneumogastriacs in the neck is followed by quickening of the heart's rhythm. Stimulation of the central end of one of the divided nerves has no effect; if the peripheral end be acted on, the heart's action is slowed, and finally stopped altogether. If, before the division of these nerves, the cervical sympathetic be cut across, and also the spinal cord below the medulla, the usual acceleration does not follow. To explain these phenomena the existence of a cardio-inhibitory centre in the medulla has been recognized, from which impulses descend to the inhibitory ganglia of the cardiac wall, along the fibres of the pneumogastric. Its action is determined by reflex impulses conveyed from various parts of the body as already exemplified. And it probably is, in its turn, inhibited by certain influences arriving from other quarters, as we know takes place with regard to other centres. In contradistinction to Weber's theory of *inhibition*, Moleschott and Schiff advocate the theory of *exhaustion*. They affirm that slight stimulation of the pneumogastric nerve is followed by quickening of the heart's action, while a strong stimulus slows it. Accordingly they look upon the vagus as a motor nerve of the heart, but easily excited and soon exhausted, and to its exhaustion they attribute the slowing of the cardiac movements.

Heart Poisons.—Certain poisons have a striking influence on

the heart. To explain their manifestations it has been supposed that the pneumogastric nerve terminates by communicating with the inhibitory ganglionic centre or centres in the cardiac wall. In *urari* poisoning, the inhibitory influence of the vagus is lost, but inhibition may be obtained by electric stimulation applied directly to the sinus. In *atropin* poisoning the inhibitory action is completely lost, so that no method of stimulation will have the effect of producing arrest of the cardiac contractions. The application of *muscarin* or *pilocarpin* brings the heart to rest in a state of wide diastole, but activity is at once restored by the use of atropin, and again destroyed by the use of pilocarpin (not by muscarin). The application of pilocarpin (or jaborandi) to the surface of the ventricle stops its contractions, whilst the auricles go on as before. *Nicotin* slows, and then stops, the heart's action, but its action is transitory. The inhibitory action of the vagus will then be found to have disappeared, but the contractions are stopped by the use of muscarin, and again by atropin. The action of nicotin is prevented by the previous administration of atropin. *Physostigmin* also slows and stops the heart's action. *Upas antiar* and *veratrin* excite powerful tetanic contraction of the ventricles. These results have been explained by suggesting that *urari* paralyses the ends of the vagus fibres, while nicotin first stimulates and then exhausts them; atropin paralyses the inhibitory ganglionic cells, while muscarin and pilocarpin stimulate them, &c.

Accelerator nerves.—Certain nerve fibres have been described, the stimulation of which is followed by quickening of the rate of the heart's action. Stimulation of the sympathetic trunk, or of its peripheral end after section, is followed by acceleration of the heart's action; section alone by slight retardation (V. Bezold). They have been found to travel with the vertebral artery, and emerge from the sympathetic ganglia to pass towards the heart. One has been described arising from the last cervical ganglion—the third branch in the rabbit, the second in the dog (*accelerator nerve of Schmiedeberg*); another from the first dorsal ganglion (*accelerator nerve of Cyon*). The action of these nerves presents many striking peculiarities. The latent period is very long, and it may take as much as ten seconds to reach the maximum rate of beat under stimulation. The decline, after the removal of the stimulus, is slow, so that a considerable time is required before the normal rate is attained.

They are completely controlled by the vagi, so that stimulation of the latter has the effect of slowing the heart's action during the activity of the accelerator nerves, as readily as if no other influence were at work. When, however, the vagus stimulation ceases, the original rate of acceleration is rapidly re-attained. The influence of these nerves is not removed by the action of any of the heart poisons enumerated above; it is,

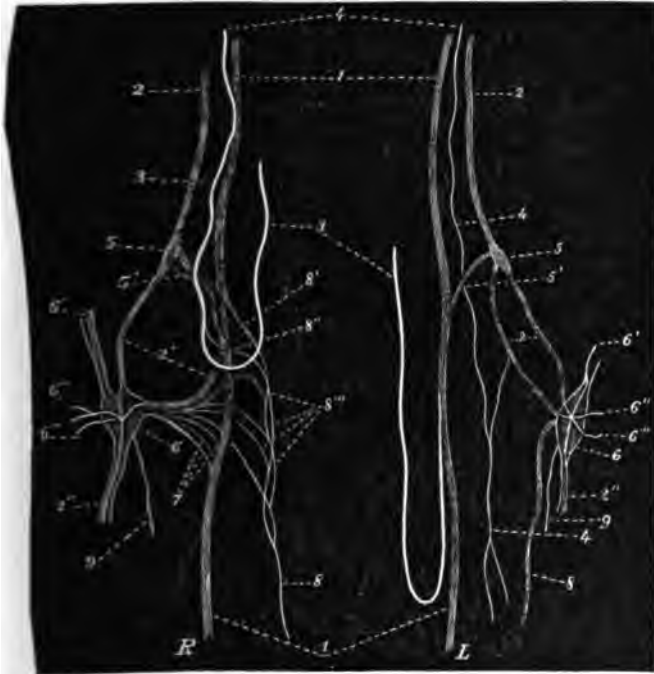


Fig. 25.

PLEXUS CARDIACUS AND GANGLION STILLATUM OF THE CAT.

(R) right, and (L) left; $1\frac{1}{2}$ natural size.

- | | |
|---|--|
| 1. N. Vagus. | 5'. Communication between vagus and cerv. m. |
| 2. Cervical sympathetic. | 6. Ganglion stellatum (first thoracic g.). |
| 2'. Com. branches between middle cervical ganglion and g-stellatum. | 7. Com. branches with vagus. |
| 2''. Thoracic part of sympathetic. | 8. N. accelerans. |
| 3. Recurrent laryngeal. | 8, 8', 8''. Roots of n. accelerans. |
| 4. Depressor nerve. | 9. G. Stellatum. |
| 5. Middle cervical ganglion. | |

however, greatly affected by temperature, as at low temperatures the action is slight and slow to appear, whilst as the temperature rises the action is more easily provoked, as well as being more pronounced. Their influence is compared by Baxt to that of heat; according to him it quickens the systole as well as shortening the diastole. What is gained in speed is, however, always lost in force, as no increase of the blood-pressure takes place under the influence of these nerves: rather, indeed, a diminution in some cases. The effect of stimulation on the tracing is shown in the figure on page 177. The interval between A and B shows the gradual quickening of the heart beats.

The accelerator fibres arise in the upper part of the spinal cord; for stimulation in this region quickens the heart's action after section of the cervical part of the cord and of the sympathetic, pneumogastric, depressor, and splanchnic nerves on both sides in a curarised animal, while artificial respiration is maintained. In this case it cannot be due to reflex action, as the nerves of the neck are divided, nor can it be due to any influence on the blood-pressure after section of the depressor and splanchnic nerves. Stimulation of the cord at various heights produces acceleration of the heart's action (V. Bezold), but this is merely due to vaso-motor action, as it takes place even after destruction of all the cardiac nerves (Ludwig and Thiry). Stimulation of the two first dorsal ganglia of the sympathetic quickens the heart's action, and the accelerator fibres also come from the cord—with the *rami communicantes* (Cyon), or *anastomosis of Vieussens* (Schmiedeberg). According to Schiff all the accelerator nerve fibres are contained in the pneumogastric. Some pass into it from the spinal accessory, leave with the superior laryngeal, then enter the anastomosis of Galen, recurrent laryngeal, and cardiac plexus.

Cardiac Nerve-Centres.

The extra-cardiac centres which preside over the movements of the heart are situated in the upper part of the medulla spinalis, and probably in the bulb itself. If the intervention of the inhibitory centre be cut off by section of the pneumogastrics, that of reflex action by section of the sympathetic in the neck, and the vascular pressure be at the same time lowered by section of the splanchnics, or of the cord above the level of their origin, stimulation of the upper part of the

spinal cord will be followed by acceleration of the beats of the heart (V. Bezold, Cyon).

The *inhibitory centre* is situated in the medulla oblongata, but its situation has not been precisely determined. Galvanisation of the medulla oblongata arrests the heart's action (Budge).

The cardiac centres are influenced by two factors : (1) the state of the blood : (2) nervous agency.

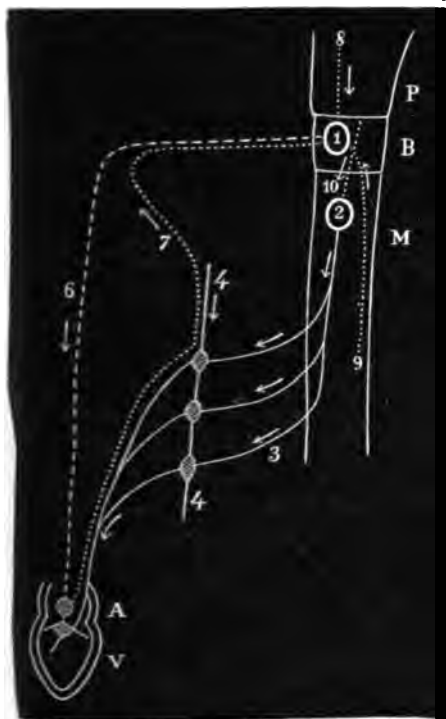


Fig 26.

DIAGRAM OF CARDIAC CENTRES (after Beaunis).

P, Pons Varolii. B, Bulb (medulla oblongata). M, Medulla spinalis (upper part). 1, Cardio-inhibitory centre. 2, Accelerator centre. 3, *Rami communicantes*. 4, Sympathetic trunk. 6, Pneumogastric. 7, 8, 9, Course of centripetal fibres, which stimulate the cardio-inhibitory centre. 10, Centripetal nerves, which stimulate the accelerator centre.

(1) The results of experiments go to prove that the accelerator centre is stimulated by oxygen, and the inhibitory centre by carbonic acid, and the preponderance of either gas in the blood manifests the corresponding influence on the action of the heart.

(2) The cardiac movements are influenced by reflex stimulation from the other nerves. (a) Stimulation of the nerves of common sensation ; e.g., crushing a frog's foot stops the heart's action (Foster). A smart tap on the abdomen of a frog has the same effect (Goltz), and so has even touching the inflamed intestine (Tarchanoff). (b) Powerful emotions are known to cause inhibition, or even complete cessation of the movements of the heart. Feeble stimulation of some sensory nerves is sometimes followed by quickening of the heart's

action. Stimulation of the central end of a muscular nerve has the same effect (Asp).

Sensory Nerves of the Heart.—In the normal state the sensation of the heart is *nil*; touching or pricking the heart causes no pain, a fact long ago known to Harvey. Still it is influenced by irritation of sensory nerves, of which the one whose action is most obvious is the *depressor* nerve, to be described more fully later on. Irritation of its central end causes a reflex slowing of the heart's action, through the agency of the pneumogastric, as well as a fall of arterial pressure, from dilation of the peripheral vessels. At the same time, the amplitude of the respiratory movements is increased, and even painful sensations are felt.

After section of both depressor nerves, irritation of the endocardium, by application of a concentrated solution of chloral hydrate, produces arrest of the respiratory movements; this arrest does not occur after section of the pneumogastric nerves close to the base of the skull—showing that sensory fibres are contained in the vagus trunk itself (Francois-Franck).

Innervation of the Blood-vessels.

The smooth muscle cells of the arterial coats are supplied by the so-called *vaso-motor* nerves, most of the fibres of which appear to come from the sympathetic chain, but of which the real origin must be sought farther off. The knowledge of the existence of this system of nerves dates from the discovery by Claude Bernard (1852), that section of the cervical sympathetic was followed by dilation of the blood-vessels and elevation of temperature on the corresponding side of the face, while galvanic stimulation was followed by the opposite results. He also observed that certain vascular nerves have the opposite influence (e.g., chorda tympani), the stimulation of which causes vascular dilation, and, for the two classes of nerves, Schiff has proposed the names of *vaso-constrictor* and *vaso-dilator* respectively.

The vascular dilation is still better marked in the neck, if the superior cervical ganglion be removed, than in case of simple section; but, in either case, the effects are transitory (24 hours after section, 15-28 hours after removal). The results are still more pronounced if the auricular is magnus nerve be divided at the same time (A. Moreau). The dilation of the blood-vessels has been observed in the deep parts also: in the membranes of the brain (Nothnagel, Goujon), in the mucous membrane of the

tympanum (Prussak), in the choroid (Sinitzin). Donders has, however, failed to detect any dilation of the vessels of retina or choroid.

The most important of the vaso-motor nerves of the body are undoubtedly the splanchnic; their ramifications supply nearly all the abdominal blood-vessels, and, after section within the thorax, the abdominal viscera become engorged with blood, a very large proportion of the blood of the body is turned in this direction, and the pressure is lowered in other parts of the circulation. But, even here, the results are merely temporary, the normal tone of the vessels is soon restored (long before the nerves have time to become re-united). The vaso-motor nerves of the liver may be traced pretty high up the sympathetic chain; stimulation of the annulus of Vieussens was found by Cyon and Aladoff to produce contraction of the hepatic vessels, the surface of the organ becoming pale, and covered by whitish spots.

The spinal nerves contain vaso-motor fibres, which come partly from the spinal cord, partly from the sympathetic chain. Section of the great sciatic nerve is followed by dilation of the blood-vessels of the lower limb, and, similarly, division of the brachial nerve-trunks causes vaso-motor paralysis in the upper extremity.

The influence of the spinal cord on the circulation was first noticed by Nasse (1839), who observed an elevation of temperature in the limbs after section of the cord. Brown-Sequard (1852), demonstrated that division of the lateral half of the dorsal portion of the cord was followed by elevation of temperature in the hinder limb of the corresponding side. Galvanisation of the cord produces the opposite result, and causes diminution of the calibre of the corresponding arteries (Pflüger). Stimulation of the spinal cord at the level of the atlas produces contraction of all the branches of the aorta; this contraction is best marked in the renal arteries (Ludwig, Thiry). The diminution of calibre is not noticeable in the muscular arteries (Hafiz).

Electric stimulation of the medulla oblongata in the frog causes constriction of the arteries of the tympanum and of the inter-digital membrane (Stricker and Kessel); and Budge, by stimulation of the crus cerebri of the rabbit, has produced contraction of all the arteries of the body.

On the subject of the localization of the vaso-motor centres,

great discrepancy of opinion exists. Owsjannikow places the vaso-motor centre in the upper part of the medulla oblongata, reaching from 1 or 2 mm. below the tubercula quadrigemina to 4 or 5 mm. above the calamus scriptorius, and nearer to the anterior than to the posterior surface. Schlesinger, on the other hand, without denying the existence of a main centre in the medulla oblongata, believes that vaso-motor centres are distributed along the whole length of the spinal cord. Dittmar localizes the centre in the medulla oblongata, in the antero-lateral nucleus of Lockhart Clarke, while the vaso-motor fibres pass from this centre along the lateral column of the spinal cord (Nawrocki). A few authorities have admitted the existence of vaso-motor centres in the cortex cerebri.

In addition to the cerebro-spinal centres, the existence of peripheral vaso-motor centres has been admitted by some of the best observers. The question still remains very obscure. Small ganglionic enlargements have been seen on vaso-motor nerves in some situations (Arnold, Henocque), and they have been supposed to preside locally over the contraction of the muscular fibres of the arterial walls.

With regard to their physiological action, the vaso-motor centres seem to be in a state of constant activity; nervous impulses are continuously passing to the muscular fibres of the walls of the vessels, under the influence of which the latter are maintained in a state of moderate tonic contraction (*tonus vasculaire* of Vulpian).

The *variations of temperature* proceed, *pari passu*, with the variations of calibre of the blood-vessels. Vaso-motor paralysis produces elevation of temperature, and stimulation of the same nerves causes depression. These results were, at first, regarded by Claude Bernard as due to a direct influence of certain nerves (*nerfs calorifiques*); but it is now known to be due merely to the changes in the quantity of blood passing through the corresponding region.

The influences of the *emotions* (shame, fear, anger, &c.) on the vaso-motor nerves is too well-known to require detailed description.

Vaso-dilator Nerves.—Claude Bernard was the first to remark that stimulation of the chorda tympani nerve produced dilation of the vessels of the submaxillary gland. The subject was subsequently taken up by Schiff, who came to the

conclusion that there were two kinds of vascular dilation—(1) the *neuro-paralytic*, due to paralysis of the ordinary vaso-motor nerves, and (2) *active* dilation, produced by the influence of certain hypothetical nerve-fibres to which he gave the name of vaso-dilator. Stimulation of the glosso-pharyngeal has the same effect on the posterior segment of the tongue, that section of the chord tympani has on the submaxillary gland and anterior segment (Vulpian). Stimulation of the *nervi erigentes*, which come from the three upper sacral nerves, cause erection of the penis in the dog. Two theories have been advanced for the explanation of these facts: (1) the *active dilation* of Schiff; (2) the *passive dilation* of Claude Bernard. With regard to the hypothesis of an active dilation, Schiff himself does not offer any explanation of its mechanism, although he believes in its existence. That an increase of the peristaltic movements of the arterial coats takes place, is an explanation advanced by Legros and Dorimus, but it has not been substantiated. An active elongation of the muscular fibres of the arterial wall is the hypothesis advanced by Grünhagen, who bases this idea on the analogy of the dilation of the pupil.

The passive dilation is admitted now by most physiologists, but the explanation of its mechanism differ. Some have suggested that constriction of the veins takes place, but they are dilated, in some instances, at least (as in case of the submaxillary gland). Some think there is an increased attraction between the blood and tissues (*vis a fronte* of Brown-Sequard and Vulpian), but this has been found to be purely hypothetical. An inhibitory action has been attributed to the vaso-dilator nerves by Claude Bernard, Rouget, and Vulpian, who attribute their effects to a transitory paralyzing influence exerted over the vaso-motor fibres by ganglia, which are placed on the course of the vaso-dilator nerves. Goltz has recently attempted to generalize the actions of vaso-dilator and vaso-constrictor nerves. He admits the existence of peripheral ganglia distributed along the course of the vessels whose function it is to preside over the vascular tonicity. They are influenced by the medullary centres, as those of the heart are by the medulla oblongata. The vaso-dilator fibres exercise an inhibitory action on these, and the coats of the vessels then yield to the internal pressure when the action of the constrictor nerves is suspended.

So far as experiments on the subject can teach, the vaso-

constrictor nerves travel chiefly with the sympathetic, and the vaso-dilator with the cerebro-spinal nerves, but to this rule there are many exceptions.

Of all the vaso-dilator nerves, the one whose influence is most widely extended is the *depressor nerve* of Cyon. It was discovered by this physiologist in the rabbit, arising by two roots—one from the pneumogastric trunk, the other from the superior laryngeal. On stimulation of the central end of this nerve a lowering of arterial pressure follows, and a diminution of the frequency of the pulse. There is no direct connection between these two consequences, for if the pneumogastric nerve be divided before the depressor, the diminution of pressure results without any change in the rate of the pulse. The same consequences take place whether the animal is or is not curarised; and, if all the connexions of the heart with the spinal cord and brain be cut off, the depression is the same, proving conclusively that it is not dependent on any change of the heart's action. The stimulation seems to be conveyed up to the vaso-motor centre in the medulla oblongata, which it inhibits, and the consequent lowering of vascular tone is followed by the fall of blood-pressure. According to Stilling, this nerve acts only on the blood-vessels of the abdomen and inferior extremities; after compression of the aorta below the diaphragm, section of the splanchnic nerves, or section of the spinal cord at the level of the third dorsal vertebræ, stimulation of the depressor nerve is followed by no diminution of pressure in the carotid.

Peculiarities of Circulation in different parts.—Brain. For the performance of its all-important functions this organ requires a very large supply of blood. Uniformity of quantity is preserved by the passage of the large trunks through unyielding bony canals, by free inosculation at the base, and tortuosity of the branches as they pass along the surface. To prevent the throbbing movements of the large vessels causing pressure on the delicate nerve structures, the arteries all break up in the pia mater before entering the brain substance. Accordingly, in the substance of the cerebral mass there is no true anastomosis, the communication between adjacent arterial districts being only by means of capillaries, and the occlusion of a considerable trunk beyond the circle of Willis is almost necessarily followed by starvation of the part to which it is distri-

buted. Arteries which terminate in this way have been described by Cohnheim as terminal arteries (*End-arterien*).

In *erectile tissue* the capillaries dilate and form cavernous spaces which are capable of holding large quantities of blood. When the afferent arteries are dilated they are also capable of accommodating large quantities of blood, and, accordingly, the organs which are formed of this tissue are capable of great increase of size under certain nervous influences.

Some of the abdominal viscera, especially the spleen, present peculiarities of circulation, which will be studied when we come to examine the structure of these organs.

CHAPTER VII.

LYMPH.

THIS fluid may be conveniently obtained from the lymph-sacs of the frog, or from the thoracic duct, or one of the leading lymphatics of the limb. Human lymph has been obtained only from lymphatic fistulæ.

It is a colorless or slightly opalescent fluid of alkaline reaction, the alkalinity not being so well marked as that of the blood; it has a characteristic odor, and a dull saline taste, followed by an alkaline after-taste. It is found on examination to consist of a clear fluid, in which white corpuscles, like those of the blood, float in large numbers. The specific gravity is 1.045. It coagulates after removal from the vessels.

Corpuscles.—The lymph globules are identical in all their characters with the white corpuscles of the blood, and accordingly do not require a separate description. In addition, however, to these, free nuclei are found, and small cells containing a large number of granulations. The mode of formation of these corpuscles is not well understood, but there is no doubt that they originate chiefly in the lymphatic and vascular glands, and in adenoid tissue elsewhere. They are said to be also formed by division of the fixed connective tissue corpuscles (His), from the epithelium of lymphatics and lymphatic cavities (Bilroth, Frey), and from the epithelium of serous membranes (Schweigger-Seidel). Once formed, they seem to have the power of multiplying by fission (Ranvier). They subsequently become the white corpuscles of the blood, but a large number probably break up and disappear.

The *plasma* of lymph is an alkaline fluid of a citron-yellow or amber color, and sometimes almost colorless; like that of blood, it separates after withdrawal from the vessels into a clot and serum.

Fibrin obtained from lymph has the same properties as that of blood. It is sometimes absent, and the lymph then has not the power of coagulation, as is usually the case before it passes

through a lymphatic gland. Lymph from the thoracic duct contains about two parts per thousand.

Lymph-serum has nearly the same chemical composition as that of blood, the proportions only differing. It contains three per cent. of albuminoids, especially globulin, serum-albumen, a little albuminate of potash, and an excess of fibrinogen and peptones are also present; nitrogenous extractives, urea in greater proportion than in case of blood-serum (Wurtz); fats in the state of glycerides of the acids: oleic, palmitic, butyric; traces of soaps and of volatile fatty acids, especially butyric; cholesterin, lecithin. Glucose is believed by some to be always present, but according to C. Bernard it is found only when the system is saturated with this sugar. Of mineral substances, potash and phosphates abound in the clot, and soda in the serum. Carbonates and sulphates are also present, and a small proportion of oxide of iron.

Gases.—The gases of lymph consist almost entirely of CO₂, with a small quantity of N and traces of O (Hammarsten). It contains more CO₂ than does the arterial blood, and less than venous. The following table gives the proportions for 100 parts of lymph (from the dog):—

Lymph from fore limb	O —	CO ₂	41.89	N ₂	1.12
" "	.10		47.13		1.58
" chiefly from the limbs	—		44.07		1.22
" from limbs and from intestine	I		37.55		1.63

The coagulation of lymph is a little slower than that of blood, and the clot is proportionally very small. Its weight is about 1-25th that of the lymph; it is soft, whitish, and possessed of little elasticity. It sometimes reddens at the end of a short time; this change of color is said by some not to take place in pure lymph, but to be due to the presence of some red blood corpuscles from venous regurgitation; or it may be due to some chemical change produced by the exposure to oxygen (Gubler and Quevenne).

The *quantity* of lymph has been estimated by some authorities from the amount collected from the thoracic duct in a certain time, but such calculations can have no value whatever. It has been calculated by some to be one-tenth of the weight of the body; Ludwig estimates it at about one-fourth, and Krause as much as one-third. The proportion is certainly very large: Colin has obtained two kilogrammes in one hour from the horse.

The following table from Schmidt gives the composition of lymph from the neck and of chyle from the thoracic canal of a colt fed on hay (per 1000 parts):—

	Lymph.	Chyle.	Serum.		Plasma.	
			Lymph.	Chyle.	Lymph.	Chyle.
Water	955.36	956.19	957.61	958.5	907.32	887.59
Solids	44.64	43.81	42.39	41.5	92.68	112.41
Fibrin	2.18	1.27	—	—	48.66	38.95
Albumin	34.99	35.11	32.02	31.63	34.36	67.77
Fat			1.23			
Extractives... }			1.78			
Mineral Salts ...	7.47	7.49	7.36	7.55	9.66	5.46
Chloride of sodium	5.67	5.84	5.65	5.95	6.07	2.30
Soda	1.27	1.17	1.30	1.17	.6	1.32
Potash	.16	.13	.11	.11	1.07	.7
Sulphuric acid ...	.09	.05	.08	.05	.18	.01
Phosphoric acid ...	.02	.04	.02	.02	.15	.85
Earthy phosphates	.26	.25	.20	.25	1.59	.28

There is no analysis of pure human lymph, and our knowledge of its composition has been derived from the fluids collected from lymphatic fistulæ. The following are the principal analyses which have been obtained :

Water ...	939.87	934.77	969.26	957.60	940.95	986.34	943.58
Solids ...	60.13	65.23	30.74	42.40	60.50	13.66	56.42
Fibrin ...	.56	.63	5.20	.37	1.65	1.07	1.60
Albumin ...	42.75	42.80	4.34	34.72	—	2.30	21.17
Fats ...	3.82	9.20	2.64	—	—	1.50	24.85
Extractives	5.7	4.46	3.12	—	—		1.58
Salts ...	7.3	8.20	15.44	7.31	—	8.79	7.22

An examination of the following analyses shows that, in passing through the walls of the capillaries, blood-plasma loses about one-half of its albumin and two-thirds of the fibrin ; the other constituents remain in nearly the same proportion.

	Plasma of blood, P. of lymph. P. of chyle.		
Water, per 1,000 parts	901.50	957.61	958.50
Fibrin ..	8.06	2.18	1.27
Albumin ...	81.92	32.02	30.85
Salts ...	8.51	7.36	7.55
Chloride of sodium	5.546	5.65	5.95
Soda ...	1.532	1.30	1.17

The lymph which is originally derived from the blood-plasma is carried back again to be poured into the general circulation by a series of vessels, called *lymphatics*, which converge to form the so-called *thoracic duct*. The lymphatics of the right side of head, neck, and upper extremity converge to form a small duct, the *ductus lymphaticus dexter* of Steno, which terminates at the corresponding point on the right side (junction of subclavian with internal jugular vein).

The lymphatic vessels commence in the connective tissues, in one of two modes—the *plexiform* and the *lacunar*. The former is merely a dense capillary mesh work, and the open mouths of the minute vessels in the latter communicate with the spaces between the connective tissue corpuscles. From the chinks between the latter the lymphatic capillaries lead off: the walls being at first formed of a single layer of endothelial cells, the chief difference between them and the blood capillaries being the larger size and greater irregularity of calibre of the former. As the lymphatics increase in size, they receive coats like those of the small veins, only differing in their greater thinness and more numerous distribution of valves, above each pair of which there exists a dilation: so that one of these vessels, when distended, presents a somewhat beaded appearance. Nearly all the lymphatics, before joining the thoracic duct, pass through one or more lymphatic glands.

Lymphatic Glands.—A lymphatic gland is usually of somewhat reniform outline. It is invested by a fibrous capsule, which presents a considerable proportion of elastic fibres, and from the deep surface of which fine processes (*trabeculae*) pass inwards, and, interlacing, split up the interior of the gland into a coarse meshwork. This fibrous meshwork is the *connective tissue nucleus of hilus stroma* of His. On making a section through the substance of a lymphatic gland, the alveolar spaces are found to be more open towards the surface, and this part of the gland is called the *cortical* portion; while the central structure, which is made up of smaller spaces, is known as the *medullary* part. The alveoli contain the proper gland substance which, in the cortical portion, forms somewhat pyriform nodules, while it is prolonged into rounded cords in the medullary part. The former are called *lymph-follicles*, the latter *lymph-tubes* (*medullary tubes* of His). Both are connected to the surrounding trabeculae by retinacular fibres, which are very loosely arranged, and so com-

paratively open spaces between and around the retinacula form the *lymph-path* (*lymph-sinus* of His), so called because it is traversed by the current of lymph, which is continually passing

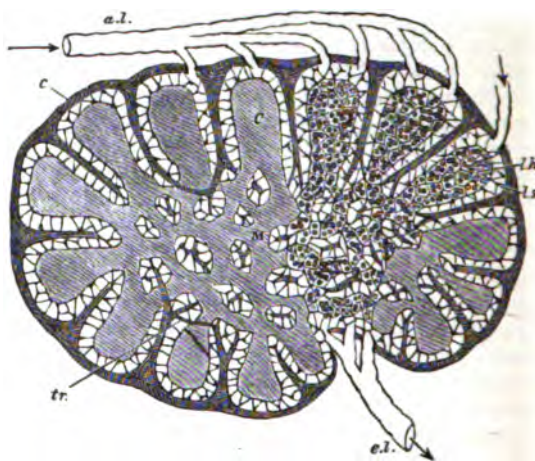


Fig. 27.—Diagrammatic Section of Lymphatic Gland.

a. l. afferent; *e. l.* efferent lymphatics. *C.* cortical substance. *M.* reticulating cords of medullary. *l. s.* lymph-sinus; *c.* fibrous coat sending trabeculae *tr.* in the substance of the gland.

through the interior of the gland. The loose space around each follicle is called by Frey, the *investing space of the follicle*. When a hilus exists, the nutrient blood-vessels are found in this situation, and the *efferent* lymphatic vessels (*vasa efferentia*) pass out in the same place. The *afferent* lymphatics (*vasa afferentia*), which are larger in number, but individually smaller in size than the efferent vessels, enter the gland on the opposite side.

The lymph-follicles and tubes, as already mentioned, form the proper gland substance, which is made up of a very delicate form of connective tissue, which has received the several names of *lymphoid*, *retiform*, *adenoid* (His), or *cytogenous* (Kölliker).

It is formed of an excessively fine meshwork of interlacing fibres, in the interspaces of which lymph-corpuscles are closely packed. In the centre of each lymph-tube an artery and vein are found, which form a capillary plexus within the lymph-follicle. The lymph-path contains some corpuscles, which seem to pass out from the follicles and tubes.

On meeting the surface of the gland, the afferent lymphatics lose all their coats, which become blended with the tissue of the gland capsule. The endothelial lining is prolonged into the lymph-path, the spaces of which it lines, and in this way becomes continuous with the endothelium of the efferent vessels.

The current of lymph which is conveyed to the gland by its afferent vessels is thus transmitted along the lymph-path through the interior of the gland, and is carried off on the other side by the efferent vessels. In this course it washes away large numbers of the lymph-corpuscles. Accordingly, after passing through a lymphatic gland, the lymph is found to have become much richer in corpuscles, and to have acquired the power of coagulation, which it had not possessed previously. The source of these lymph-corpuscles, which are being formed continually in great numbers in the system, is still somewhat obscure. Frey believes that they come from the walls of the lymphatic vessels and of the lymph-paths which lie within the glands, from which they are washed away by the lymph-current. Beaunis thinks that they come from the nuclei, which are placed at the nodes of intersection of the fibres which form the meshwork of the adenoid tissue of the lymph-follicles and lymph-tubes. His believes that they may be derived from proliferation of the fixed connective-tissue corpuscles. That they are also derived from the endothelium of serous membranes is maintained by Schweigger-Seidel, who thinks that, after being formed and detached, they pass out through the stomata into the lymphatic capillaries.

The circulation of lymph is maintained chiefly by the *vis a tergo*, derived from the heart, as it comes directly from the fluid part of the blood which is continually oozing through the capillary walls, and each succeeding part of the fluid displaces the portion that had just previously escaped. Passing into the lymphatic vessels the flow is perhaps slightly aided by the mus-

cular and elastic tissue in the coats of the latter. The progress of the lymph-current is materially aided by the movements of the surrounding muscles, the pressure of which causes diminution of the calibre of the vessels ; while regurgitation is prevented by the presence of the closely-set valves. On passing into the thoracic duct, the flow is hastened by the inspiratory movements, and, according to some, by the pulsatile movements of the aorta ; while the passage of the contents of the duct into the sub-clavian vein is facilitated by the direction of the current of blood within the latter vessel, where the duct joins it nearly at a right angle.

CHYLE.

The chyle is the fluid taken up by the intestinal lymphatics so-called *lacteals*) from the interior of the alimentary canal during digestion. The lacteals, which were first noticed by Gaspard Asselli (1622), received this name from the milky appearance of the fluid which they carry during digestion. Except at this time, their contents are found to be identical with those of the other lymphatics.

Chyle contains the same anatomical elements as lymph, and in addition, contains innumerable fine granules (the *molecular base* of Gulliver). These minute particles are no other than the particles of emulsified fat, each of which is invested by an albuminous coating (*haptogenous membrane* of Ascherson and Müller).

The chemical composition of chyle is nearly that of lymph ; it differs especially in being richer in solid matters, particularly in fats. Besides the neutral fats, it contains small quantities of soaps, and the proportion of each varies according to the particular period of digestion. Peptones are also present, and traces of urea. According to some authorities, glucose is always present ; others say that it can only be found after ingestion of saccharine food, and that the quantity is always in proportion to the amount of the latter taken into the alimentary canal. The gases of chyle are the same as those of lymph.

The following analyses, by Hoppe-Seyler, are of the chyle found in the peritoneal and pleural cavities of a man, after rupture of the thoracic duct :—

LYMPH.

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I.		Soluble Salts : . .		6.804
Water (per 1000)	940.724	Insoluble „	. . .	.350
Solids	59.276	II.		
Albuminoids	36.665	Fibrin	. . .	6.045
Cholesterin	1.321	Globulin	. . .	2.832
Lecithin	.829	Serum-albumin	. . .	38.968
Fats	7.226	Fats	} . .	4.709
Soaps	2.353	Cholesterin		
Alcoholic extract	3.630	Lecithin		
Aqueous	.578			

CHAPTER VIII.

PHYSIOLOGY OF THE TISSUES.

THE first great obvious division of the structural elements of the animal body, and one of the most important from the physiologist's point of view, is by separating them into two varieties—the superficial and the deep. The first includes the epithelial structures; the second all the other tissues. Of the latter there are two varieties of tissue whose structure and functions are of pre-eminent complexity; these are the *muscular* and the *nervous*. The interspaces between the different masses of these tissues are filled up by the various forms of the so-called connective tissues.

(A) Epithelium.

Epithelium is formed by one or more layers of cells arranged on the surface of homogeneous membrane (*basement membrane* of Todd and Bowman), with a subjacent vascular stratum. When there is but a single layer of cells the epithelium is said to be *simple*; when there are two or more layers it is said to be *compound* or *stratified*. The component cells in every case are cemented together by an albuminous semi-fluid substance, the limits of which are best demonstrated by the action of nitrate of silver. No other variety of tissue is found between the epithelial cells, excepting nerve fibres, of which the terminal filaments may often be traced into epithelial tissues. There are several varieties in the shape of epithelial cells; some are polyhedral or spheroidal, in which all three dimensions are nearly equal; some are conical or cylindro-conical, in which the vertical measurement predominates; some are flattened, so as almost to present but two dimensions. In some instances vibrating fibrils (*cilia*) project from the free surface of the cell (ciliated epithelium). In other situations tooth-like processes spring from the surface of the cells to meet similar processes from neighbouring cells, and so limiting spaces through which the plasma of the blood is allowed to trickle and supply the

necessary nutritive material (*prickly cells* of Max Schultze). These cells are found in the deeper layers of the epidermis, and of the lingual epithelium. In certain places a variety of epithelium is found, which is formed of a single layer of tessellated cells laid edge to edge without overlapping; this is the *endothelium* of His. Endothelium, properly so called, is developed from the mesoblast, but epithelium having similar microscopic characters is found in the air-vesicles of the lungs.

Epithelium forms a continuous covering over all the surfaces of the body, and accordingly every substance which penetrates into the organism has to pass through an epithelial membrane. The different forms of epithelium may be divided into the (a) *simple*, and (b) *stratified*. Of these the first is made up of a single layer of cells, which displays (in the flattened form) but a moderate amount of physiological activity. The nutritive energy displayed by the columnar cells is much greater, and it reaches its maximum in the stratified epithelium.

(a) 1. *Flattened, squamous, or tessellated epithelium*: composed of a single layer of cells laid edge to edge, and accordingly resembling the endothelial cells found in blood-vessels, &c. This variety is found in the air vesicles of the lung, and in the glomeruli of the kidney.

2. *Columnar or cylindrical*: formed of cells having a cylindrical or cylindro-conical shape, but more generally found reduced to a prismatic form by mutual pressure. This epithelium is found in the stomach, intestine, gland-ducts, &c.

3. *Ciliated*. This variety of epithelium, formed of columnar cells with vibratile processes, is found in the small bronchi, &c.

(b) 1. *Stratified squamous epithelium*.—This variety is made up of numerous layers of cells, of which the most superficial are quite flattened, the deeper larger and polyhedral, and bearing tooth-like processes, while the deepest layer is made up of cylindrical cells.

2. *Stratified ciliated epithelium*.—In this form the deep cells are of round or oval form, while the superficial, which alone are provided with cilia, are of cylindrical shape. This variety is found in the larynx, trachea, bronchi.

The so-called *spheroidal* or *glandular* epithelium is but a variety of the columnar form. A variety of epithelium, to which the name of *transitional* has been given, is found in the urethra, bladder, ureters, and pelvis of kidney.

As derivations of the tegumentary epithelium we must regard the nails, hairs, and horny tissue. The crystalline lens is derived from the same source.

The nutrition required by epithelial cells is derived from the plasma of the blood which trickles between and around them (in case of stratified epithelium, nutritive spaces are limited by the prickly processes given off from the prominent angles, which meet those coming from neighboring cells).

With regard to the termination of *nerves* in epithelium a good deal of uncertainty still exists. Terminal nerve fibres have been demonstrated among the epithelial cells, and nerve cells have been described and figured by Langerhans in the rete Malpighii. The terminal fibrils are said by most observers to end either in fine plexuses, or in free bulbous ends, but some describe them as passing to the individual cells, and even into the nuclei (Hensen and Lipmann). Pflüger describes and figures the terminations of the nerve fibrils in the cells which line the acini of salivary glands.

(A) CHEMICAL PROPERTIES OF EPITHELIUM.

Epithelium is largely made up of the substance called *keratin*, which is also found in nails, hairs, &c., and in other structures; sarcolemma, neurilemma, Descemet's membrane, capsule of crystalline lens, basement membrane of secreting glands, capsules of cartilage cells, investing membrane of osteoblasts and of connective tissue corpuscles. Epithelium also contains a variable amount of inorganic constituents, and often a quantity of pigment, and in case of secreting glands the constituents vary according to the organ in which they are found.

Keratin is a proteid substance, which is soluble in solutions of soda and potash, insoluble in ether and in alcohol. It swells up on being treated with acetic acid, and also swells in water less rapidly. Its composition resembles that of elastin, from which it is distinguished by the presence of sulphur. Treated with nitric acid it yields oxalic acid. Heated with sulphuric acid or potash it forms by decomposition leucin and tyrosin; also aspartic acid, volatile fatty acids (acetic, butyric, propionic, valeric), and ammonia in smaller proportions. The sulphur of keratin is in a state of loose combination, and is easily given off on heating, in the form of H_2S .

A variable quantity of inorganic salts is present. In nails the chief is the phosphate of calcium. Hairs contain .5 to .7 per cent. of salts, alkaline sulphates, calcium sulphate, oxides of iron and of manganese, silicic acid.

Keratin is not found in the crystalline lens, but other albuminoids are present, of which the chief is globulin. Serum-albumin and albuminate of potash are also found.

Melanin, the granular pigment which is found in some epithelial cells (especially of the rete mucosum), also in connective-tissue corpuscles, nerve cells, lymphatic glands, &c., is a substance of which the chemical properties are not well known. Its granules are insoluble in water, alcohol, ether, alkaline and dilute acid solutions. By prolonged boiling with a concentrated solution of caustic potash they are dissolved, forming a brown coloration, which is discharged by chlorine. (This distinguishes them from particles of charcoal.)

Melanin has been supposed to be derived from the hæmoglobin, but, as Beaunis observes, a powerful argument against this notion is, that it often forms with the greatest rapidity in non-vascular portions of the organism.

(B) PHYSICAL PROPERTIES OF EPITHELIUM.

The consistence of epithelium varies with its position, increasing to extreme hardness in some exposed parts, as is seen in the hands of individuals who perform much manual work, and still more so in the formation of nails, claws, &c. That which lines the cavities of the body, on the other hand, is extremely soft and easily detached. The cohesion of epithelium is generally feeble, and examples of its yielding to moderate stretching are seen in pregnancy, &c. The elasticity of epithelium is very slight.

Epithelial tissues are *transparent*, allowing the rays of light to pass through with considerable ease; this property is of exceptionally obvious importance in the crystalline lens. They are bad conductors of heat and of electricity, and in this way the cuticle prevents the too rapid radiation of heat from the surface of the body.

Epithelial cells easily absorb water, unless covered with an oily varnish, as in case of the cutaneous epithelium, but in the latter case we see how easily the epidermis of the palms and

soles (where sebaceous glands are absent) swell up in a warm bath.

The physical laws of osmosis hardly apply to epithelial membranes. The special activity of the epithelial cells forms a modifying factor. A selective action seems to be maintained by which certain substances are allowed to pass while others are arrested. Healthy living epithelium may resist absorption, although it would be allowed to take place in the altered condition produced by disease, or by post-mortem change. The mucous membrane of the healthy bladder has been found to resist the absorption of poisonous solutions, iodide of potassium, &c. (Küss, Susini, Segalas, and others.) These results have, however, been contradicted by those of Bert and Jolyet.

PHYSIOLOGICAL PROPERTIES OF EPITHELIUM.

The nutrition of epithelium, as we have already said, is derived from the subjacent blood-vessels, from which the exuded plasma passes along the intercellular spaces (*inter-epithelial stomata*), which latter also communicate with the open mouths of the lymphatics.

The formation of certain compounds is one of the most essential properties of epithelial tissues, and this is seen with special prominence in glandular epithelium. In other cases they possess the power of extracting from the blood certain materials already existing there. The epithelial cells sometimes undergo special chemical changes by which a definite purpose is fulfilled in the animal economy; the most frequent is fatty transformation, which is one of the modes of epithelial secretion; the horny change which the superficial cells of the cuticle undergo enables it to resist the influence of air, pressure, &c.

The growth of epithelial cells is involved in considerable obscurity. The new cells are formed in the deeper parts of the epithelium, and gradually pass towards the surface, while the superficial cells are continually dropping off. Growth and repair take place so rapidly in case of the intestinal epithelium, that it has been supposed that the single layer of cells which lines the canal is regenerated after each act of digestion. Epithelial desquamation is sometimes preceded by chemical transformation, especially fatty. The mucoid degeneration of

the cell-contents of the intestinal epithelium with subsequent bursting gives rise to the appearance of the so-called *goblet-cells*.

There are two leading theories about the growth of epithelial cells; one is, that they come from pre-existing cells by multiplication; according to the other, they are always supplied by the subjacent connective tissue (called by Burckart the *matrix of the epithelial cells*). Pagenstecher makes the principal source to be the migratory connective tissue corpuscles described by Recklinghausen. Comparatively few authorities, however, favour this view. The results of *skin-grafting* are also in favor of the other theory. The crystalline lens is regenerated after removal, especially in young animals. The new lens never attains the full size of the normal one (Milliot).

Epithelium is not endowed with *sensibility*, but nerve fibres are distributed between the cells of some epithelial tissues which endow it with adventitious sensation.

D.—PROTECTIVE FUNCTION OF EPITHELIUM.

A very important use of epithelium is to afford mechanical protection to the subjacent tissues, which is so well exemplified in the cuticle which covers the surface of the body, which bears off the effects of external pressure, and also of chemical agents. The fact that it is a bad conductor of heat guards against the ill results of exposure; the hairs of the head in this way protect from insolation. The tactile sensation depends on the presence of epithelium; when this is removed, pain follows the application of anything to the surface. In a similar way the epithelium of each of the special sense organs is necessary for the exercise of its proper functions.

E.—USE OF EPITHELIUM IN ABSORPTION.

On account of the arrangement by which the whole of the surface of the body is covered by epithelium, everything which enters and leaves the organism must pass through this investing layer, and the facility with which each of these processes goes on varies directly as the other, according to the different situations of the body.

(1) The absorption of gases and of volatile substances takes place chiefly through the pulmonary epithelium, the delicate

structure of which is almost identical with that of endothelium. The intestinal mucous membrane, and even the skin, is also the seat of a rudimentary respiration. (2) The absorption of liquids and of soluble substances best exemplifies this function of epithelial membranes. Certain mucous membranes, such as the pulmonary, seem to possess almost unlimited power of absorption, while the vesical epithelium seems to resist it almost completely. The intestinal mucous membrane, which absorbs glucose and peptones so rapidly, is very slow in transmitting certain poisonous substances. Fluids are not absorbed through the skin, except after removal of the sebaceous secretion by chemical or mechanical means. (3) The absorption of fats takes place in the alimentary canal, and shall receive full consideration in connection with the subject of digestion.

F.—USE OF EPITHELIUM IN ELIMINATION.

(1) *Exhalation*.—This is the elimination of gases and volatile substances. The gases whose exhalation is of chief physiological importance are carbonic acid and water, and the elimination takes place chiefly through the pulmonary epithelium; also on a small scale by the intestine and skin, and indeed from all other epithelial surfaces, including that of the glands, as carbonic acid is found in all the various excretions.

Volatile substances which have not been isolated are also found to escape from the pulmonary mucous membrane, and in small quantity from the other epithelial surfaces, as we have such substances in the excretions.

(2) *Secretion*.—This is the special function of the epithelium of glands. The cells lining the acini are placed on the *membrana propria*, outside which is a dense capillary network. Between the latter and the *membrana propria* is a lymph space (Ludwig, Tomsa), from which it is supposed that the cells take up the elements of their secretion. Again, according to some authorities (Pflüger, Paladino), the cells of the salivary glands are in intimate connexion with the terminal filaments of the nerves, but this connexion is denied by most observers.

According to the activity of the epithelium, four varieties of the process of secretion have been described:—

(a) *Secretion by filtration or transudation*.—In this form of the secretory process the glandular epithelium forms no new

compounds, it merely takes up the materials already existing in the blood, from which it chooses the necessary substances by a selective power. To this category belongs the urinary secretion, that of the tears, sweat, &c. :

(b) *Secretion with production of new principles: s. properly so called.*—In this variety of the process the epithelium no longer acts merely the part of a filter, it modifies the substances which pass through it, and forms, at their expense, new products. Accordingly the products of the functional activity of the different glands vary, without any histological peculiarities to account for the variation. In this class may be ranged the various digestive secretions : saliva, gastric juice, &c.

(c) *Secretion by desquamation of the glandular epithelium.*—In this form the production of the secretion is dependent on the shedding of the epithelial cells, previous to which they undergo a fatty or mucous transformation.

(d) *Morphological Secretion.*—In this kind we have the additional feature of the formation of a morphological element, as in case of the formation of spermatozoa by the testicular epithelium.

CILIATED EPITHELIUM AND CILIARY MOVEMENT.

Ciliary movement was first observed by A. de Heyde, in 1683. It was carefully studied by Purkinje and Valentin, and in the present day by Calliburces and Engelmann, each of whom has devised a special registering apparatus for the purpose of measuring the velocity of the ciliary vibrations. In the case of freshly-detached epithelial cells the movement is so rapid as not to be discernible, but can be made out when the rate diminishes to about twelve vibrations per second. It presents several forms : the commonest is one of elevation and depression of the ciliary processes ; in other instances it is caused by alternate flexion and extension ; and in some rarer specimens the movement presented is one of undulation, of pendulum-like movement, or of circumduction. These varieties have been named by Valentin, respectively, *motus uncinatus* (including the first two), *m. undulatus*, *m. vacillans*, and *m. infundibuliformis*. All the cilia of a surface move in the same direction. According to Engelmann each vibration is made up of two demi-vibrations of unequal length, the longer cor-

responds to the contraction and elevation of the cilium, the shorter to its relaxation and inclination, an inclination which is due to the elasticity of the cilium itself, and is made in the direction of the general current. Klein suggests that the cilia may be direct prolongations of the longitudinal fibres of the intracellular network, and that their movements may be the effect of the contraction of the transverse fibres of the same network. These ciliary vibrations are very rapid, as many as 250 to 280 per second, and appear to be quite independent of the nervous system and of the circulation, as they persist on detached epithelial cells. Detached cilia cease to vibrate. The microscopic appearance presented by recent ciliary movements are compared by Henle to a stream of running water; when the velocity diminishes it rather gives the idea of a field of corn shaken by the wind. These movements subsist for a considerable time after death; they have been observed thirty hours or more after execution in the bodies of criminals (Ordóñez, Gosselin, Robin), and in cold-blooded animals they may persist even for several days.

The *work done* by ciliary contraction represents a considerable amount of physical labour. Thus a movement of progression was observed in a piece of the pharynx of a frog, of an area of fourteen square millimetres, after loading it with a weight of forty-eight grammes (Wyman).

Ciliary motion *sets free electricity*. Engelmann has observed on the mucous membrane of the pharynx of a frog, whilst the cilia were in motion, a current passing from the surface towards the deeper parts.

Ciliary movements are arrested or slowed by pure water, by alkalis, by acids, by dilute saline solutions, by bile, chloroform, nitrite of amyl, ether, carbonic acid, hydrogen, &c. When the movements have been arrested by neutral fluids, &c., which have not disorganised the cilia, they are restored on the addition of weak alkaline solutions. The presence of air or oxygen favors ciliary movement; but compressed air, or oxygen at a high tension, slows or arrests it. By lowering the temperature the ciliary movements are slowed; they are most active at 40° C. (104° F.), but above that point the vibration becomes slower, and are stopped (in the frog) when the temperature reaches 45° C. (113° F.) The effect of *electricity* has been differently reported: according to Kistiakowsky, Stuart, &c., both constant

and induced currents accelerate the movements, while Legros and Onimus have found a slow movement quickened by constant currents, but retarded or stopped by the induced. According to Engelmann the constant current has no effect so long as its intensity remains unchanged, while the action of the induced current varies according to the previous state of the ciliary movement. When the latter has been slow, acceleration is produced, greater for the opening than for the closing current; when the current is very powerful, the movement is retarded or completely arrested.

What the real nature of ciliary movement is, is a subject which has given rise to a great deal of discussion, but there can be no doubt that it is a variety of protoplasmic movement. Engelmann believes that it is due to a certain change of form of the elementary structures which make up the cilia. These component elements (to which he has given the name of *inotagmen*) during the time of relaxation are elongated, with the long axis parallel to that of the cilium, but in the contracted state they assume a spherical shape.

The ciliary movements in man do not seem to have any physiological use except in case of the respiratory passages, where it aids in the expulsion of mucus, particles of dust, &c.

CONNECTIVE TISSUES.

The large group of tissues included under this heading are all closely related by developmental origin as well as by structural analogy; although superficial examination may fail to detect much resemblance from the latter point of view. They may be arranged under the following heads:—

(1) Connective tissues, properly so-called—

(a) Mucous tissue.

(b) Retiform tissue (adenoid tissue of His; cyto-genous tissue of Kolliker).

(c) White fibrous tissue.

(d) Adipose tissue.

(2) Yellow elastic tissue.

(3) Cartilaginous tissue:—

(a) Hyaline cartilage;

(b) White fibro-cartilage;

(c) Yellow fibro- (elastic, reticular, or spongy) cartilage.

(4) Osseous tissue :—

- (a) Bone;
- (b) Dentine.

(1) **Connective tissues**, properly so called : (a) *Mucous tissues*. This represents the structure of embryonic connective tissue. It is formed by a homogeneous or fibrillar semi-fluid matrix, in which round or stellate corpuscles are imbedded. In foetal life it is found in the dental papillæ, and in the early connective tissue ; at birth it forms the Whartonian jelly ; in the adult it exists in the vitreous humor only.

(b) *Reticular tissue* (*adenoid tissue* of His ; *cytogenous tissue* of Kölliker ; *lymphoid tissue*). This is formed by a close mesh-work of excessively fine fibrils, in which are embedded the characteristic lymph corpuscles. At the nodes of intersection nuclei are placed, which in specimens imperfectly prepared give rise to the appearing of anastomosing cells, of which this tissue was probably originally developed. It is found in the follicles of lymphatic glands, lenticular glands of the alimentary canal, Malpighian corpuscles of spleen, &c., and a tissue exactly similar in the nervous centres forms the *neuroglia* (Virchow).

(c) *Fibrous tissue*. This tissue is formed by a fundamental substance (usually in form of fine fibrils, as in tendons, ligaments, and areolar tissue ; sometimes arranged in lamellæ, as in the cornea), in the inter-fibrillar spaces of which cells (connective-tissue corpuscles) are found. Of these some are *mobile*, and present all the appearances of leucocytes, others are *fixed*, forming an integral part of the tissue in which they are found, and presenting a great variety of shapes. In their simplest form the latter are round or oval cells, granular, nucleated, without a well-marked investing membrane, and usually found around the arteries ; there are the *perivascular cells* or *plasma cells* of Waldeyer. The osteoblasts of Gegenbaur, found in developing bone, come under this head. These granular masses of protoplasm may be fusiform in shape, as in connective tissue and in the medulla of bone, or they may present branching processes which anastomose with those of neighboring cells (*stellate corpuscles*), such as those found in the lacunæ of connective tissue, in the cornea, in growing capillaries (*vaso-formative cells* of Ranvier). When the granular protoplasm of connective tissue corpuscles disappears we have the *flattened cells* (*cellules plates*) of Ranvier,

of which we have examples in the tendon cells described by this observer.

White fibrous tissue, when examined with the microscope, is found to be made up of bundles (fig. 28) of exceedingly fine, wavy, parallel threads, of a thickness varying from about $\frac{1}{1000}$ to $\frac{1}{500}$ of an inch, and apparently homogeneous in structure. The bundles so formed may be placed parallel to one another as in tendons, or interlacing in all directions as in fasciæ or aponeuroses. The fasciculi so formed appear white when seen with reflected light, and in every case have some yellow elastic fibres mixed up with them; the latter in some cases are few, and hard to discern without special preparation, but can always be demonstrated by the action of acetic acid, which causes the white fibres to swell up and become indistinct, while the yellow fibres remaining unaffected, come prominently into view. Some of the elastic fibres are coiled round the exterior of the bundles in a spiral form (*elastic strip* of Boll), and when acetic acid is applied the white fibres swell out between, presenting a peculiar and characteristic appearance (*a, a*). The encircling fibres are sometimes arranged in form of separate rings, and the whole appearance is believed by some authorities (Ranvier, Axel Key and Retzius) to be due to the presence of an ensheathing membrane which surrounds the fasciculi, and which yields at intervals to the swelling of the white fibres, leaving small segments, annular or spiral, as the case may be. According to some distinguished authorities, the structure of these bundles is really homogeneous, and the apparent fibrillar structure is partly artificial, being the result of cleavage, and partly an optical illusion, from creasing or folding during the preparation of the specimen. The interfascicular spaces (*Saftcanälchen*

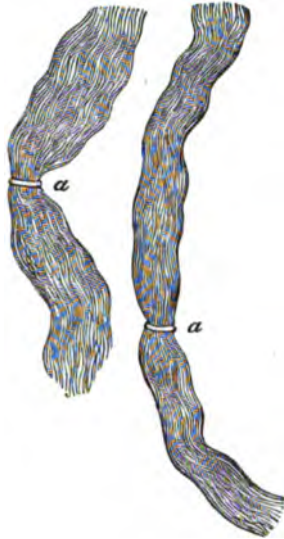


Fig. 28. - Bundles of white fibrous tissue (after Ranvier).

of Recklinghausen) lodge the connective tissue corpuscles, which do not completely fill them, but leave room for the liquor sanguinis to trickle around, and convey nutritive material to the various parts of the tissue. These spaces are in direct communication with the open mouths of the lymphatics, the branched connective-tissue corpuscles passing gradually into the flattened endothelium of the lymphatic capillaries.

If a portion of tendon be examined without special preparation, it appears made up merely of parallel wavy bundles of white fibres, presenting somewhat the appearance of skeins of silk. On cautious treatment with dilute acetic acid the delicate fibrils

swell up and become indistinct, while rows of oblong cells come into view between the parallel fasciculi. These cells are found to be formed by granular masses of protoplasm, tapering a little towards the ends, and containing each a flattened nucleus, with one or more nucleoli. The nucleus of each cell is placed near the end, and so arranged that each is close to the nucleus of an adjacent cell, so that they seem to form pairs (see fig. 29, after Ranvier).



Fig. 29.

White fibrous tissue yields *gelatine* on boiling, and contains in the recent state about two-thirds its weight of water. When dried, it becomes transparent and hard, but readily imbibes water again, and regains its original flexibility. It is inextensible, and on that account it firmly binds together the structures with which it is connected, and is of such strength that, as is well known, bones will break more easily than tendons of equal thickness.

The *blood-vessels* of white fibrous tissue are comparatively inconsiderable in size and number. In tendons and ligaments, with parallel fasciculi, they form elongated oblong meshes, the long axes of which are parallel to those of the longitudinal fibres. The *lymphatics* of tendons also form in the deep parts a close network with elongated meshes, while in the investing sheaths of the fasciculi they form polygonal meshes (Ludwig and Schweigger-Seidel).

Adipose tissue. This form of tissue is very generally distributed throughout the body, padding up the various interstices, &c. It abounds in the

subcutaneous areolar tissue, forming the so-called *panniculus adiposus*, which is specially developed in the female. It is also found in the subserous, submucous, and intermuscular planes of areolar tissue. It is collected round some of the viscera in large quantity, especially the kidneys. It rounds off the inequalities about joints, and constitutes nearly the entire bulk of the yellow marrow of bones. It is absent in the subcutaneous tissue of the eyelids, penis, scrotum, and along the middle line of the trunk. It is also absent from the lungs, and from the cranial cavity.

Histologically, adipose tissue is found to consist of cells having an average diameter of $\frac{1}{80}$ to $\frac{1}{60}$ of an inch, filled with oily matter, and imbedded in the meshes of the areolar tissue. A nucleus is present, but is pressed to one side and flattened out against the interior of the cell-wall. Fat first appears in the human embryo about the fourteenth week. Minute oil-globules first appear in the interior of some of the connective tissue corpuscles, and these eventually run together, so as to form one large drop, which, increasing in size, gradually displaces the nucleus and the original protoplasm. The latter remains as a delicate envelope, surrounding the fat-drop within the cell-wall. This deposit of fat is preceded by the formation of a rich capillary plexus, and the fat-cells come to be arranged in clusters, which in their turn unite to form lobules surrounded and connected by the fibres of the areolar tissue.

In the early years of life, fat is pretty nearly confined to the subcutaneous tissue. In the adult it is more uniformly distributed throughout the body, and collects in greater proportion about the viscera. One of the obvious changes that take place in the human female at the time of puberty, is the deposit of a well-marked layer of subcutaneous fat. In the Hottentot female the subcutaneous fat collects in large prominences over the gluteal muscles, and forms similar elevations on a smaller scale over the deltoid.

The *lymphatics* of adipose tissue accompany the blood-vessels, and sometimes completely ensheath the latter as they enter the fat-lobules.

No *nerves* have been observed to terminate in fatty tissue, although nerve-fibres pass through it on the way to their distribution.

(2) *Elastic tissue*.—The fibres of which this tissue is composed are highly elastic and extensible; but are not so strong

as those of white fibrous tissue, and it owes its usefulness in the body to its inherent power of yielding to external strain, and immediately returning to its original length when the tension has been removed. It is found in the human body chiefly in the following situations :—(1) Forming the ligamenta subflava (the purest example). (2) In the stylo-hyoid, thyro-hyoid, crico-thyroid ligaments, and true vocal cords. (3) In the middle coats of blood-vessels, especially the arteries. (4) In areolar tissues, and is specially abundant in certain parts of the subcutaneous, submucous, and subserous planes ; e. g., in the submucous tissue of the trachea, bronchial tubes ; also of the œsophagus and rectum, and in the subcutaneous tissue of the lower part of the anterior abdominal wall. In the latter situation, it chiefly forms in the male the true suspensory ligament of the penis. (5) In the cutis. (6) In capsule and trabeculæ of spleen.



Fig. 30.
Fibres of Elastic Tissue
teased out.

The constituent fibres are transparent, with well-defined, dark outline, and varying in diameter within very wide limits ($\frac{1}{1000}$ to $\frac{1}{100}$ of an inch, Schäfer). They run side by side, but frequently branching and anastomosing, forming well marked curves. When teased out they curl up at the ends in a very characteristic fashion, which has been aptly compared to the appearance of celery dressed for table. In some situations the fibres are broad and flattened, and, meeting at the edges, form lamellæ of almost homogeneous appearance, with interstices more or less closely placed (*fenestrated membrane* of Henle). In other instances again, it forms membranes of perfectly homogeneous appearance.

CARTILAGE.

This substance, the *gristle* of popular nomenclature, is an opaque substance of yellowish or pearly-white color, and translucent in thin sections. It is of firm consistence, and highly elastic, so that it easily yields to pressure, and immediately recovers its original form when the external force is removed.

These properties explain its great mechanical uses in the formation of joints.

In those situations in which cartilage occurs unconnected with the articulations it is surrounded by a fibrous sheath, known as the *perichondrium*. Of the cartilages found in the adult human body there are three varieties whose names have been given above. These are also included under the name of *permanent* cartilage, to distinguish from the varieties of *temporary* cartilage which occur in early life. Of the latter there are two varieties—the *hyaline* and the *cellular*. The latter is only found in the *chorda dorsalis* (a structure which shall receive our attention when we come to the study of development); while the former is the hyaline cartilage, destined to be replaced by the osseous structures which make up the great bulk of the skeleton. We shall consider the structure of the several varieties of permanent cartilage.

Hyaline Cartilage.—Hyaline cartilage is made up of a matrix and cells. The *matrix* has a uniform, dim appearance, somewhat like ground glass, and entirely free from fibres. The *cells* lie in cavities of the matrix, which they entirely fill, and are enclosed in transparent capsules. The latter cohere with the surrounding matrix. The individual cells are of a rounded or bluntly angular form, each containing a nucleus and one or more nucleoli. They usually occur in small groups. Towards the surface of the cartilage, the cells are flattened and arranged parallel to the surface; in the deeper part, they are somewhat oblong in shape, and mostly arranged in vertical columns.

In case of the *costal* cartilages, patches are often found in which fibres are developed; but the rest of the matrix re-

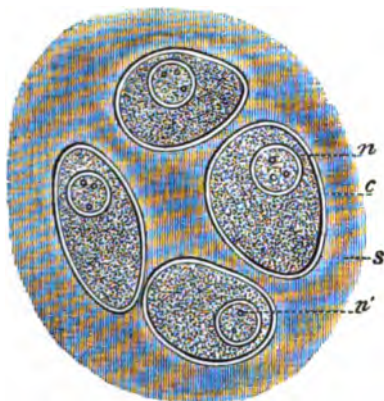


Fig. 31.—Hyaline cartilage from head of femur of frog (after Ranvier). *m*, matrix; *c*, capsule; *n*, nucleus; *n'*, nucleolus.

sembles that of articular cartilage. The deeper cells generally contain drops of oil, which, when in large quantity, displaces and obscures the nucleus.

Articular cartilage easily breaks in a direction vertical to the surface, and the broken surface appears to the naked eye vertically striated, as if of columnar structure. This has been attributed by some to the arrangement of the cells; by others, to a latent fibrous or columnar disposition of the tissue of the matrix (Leidy). It was formerly believed by some distinguished observers that a layer of epithelial cells was prolonged from the synovial membrane over the surface of articular cartilage; but such is not the case.

The *blood-vessels* form, beneath the synovial membrane around the margin of the articular cartilages, a narrow, vascular border,—the *circulus articuli vasculosus* of W. Hunter. No vessels permeate its substance. In the thicker masses, such as the rib cartilages, the vessels are conducted through canals excavated in its substance, for the supply of the deeper parts of the tissue. But the vessels do not ramify in the surrounding tissue, which, accordingly, is quite extravascular, as the canals are wide apart.

No *nerves* have been traced into hyaline cartilage, and they have been shown by experiment to be destitute of sensibility.

Chemical composition.—Hyaline cartilage contains about three-fifths of its weight of water, and yields, after prolonged boiling in water (15 or 20 hours), a characteristic constituent, named *chondrin*, which forms a jelly on cooling. It should be mentioned that this is attributed by some to an admixture of gelatin with the chondrin. Chondrin resembles gelatin in being precipitated by tannic acid, alcohol, ether, creasote, and perchloride of mercury. It differs from the latter in being thrown down by the mineral and other acids; also by alum, sulphate of alumina, persulphate of iron, and acetate of lead; each precipitate being soluble in an excess of the re-agent employed (except in case of the last).

According to Hoppe-Seyler, the following is the per-centage of water and solids:—

Costal cartilage	Water	67.67	Solids (organic)	30.13	(inorganic)	2.20
Articular „	„	73.59	„	24.87	„	1.54

The ashes from costal cartilage contained the following proportions (per 100) :—

Sulphate of potash	.	.	.	26.66
Sulphate of soda	.	.	.	44.81
Chloride of sodium	.	.	.	6.11
Phosphate of soda	.	.	.	8.42
Phosphate of lime	.	.	.	7.88
Phosphate of magnesia	.	.	.	4.55

Fibro-cartilage.—*White fibro-cartilage.* In this variety of cartilaginous tissue the matrix is formed of white fibres, in the interstices between which cartilage cells are embedded. The latter are, however, comparatively scanty in most situations. The blood-vessels are scanty, and distributed only to the fibrous parts (Toynbee). Its vital changes are slow, and, under normal conditions, it does not tend to ossify.

There are various forms met with, which are usually arranged under the following heads :—

(1) *Interarticular* fibro-cartilages. These are placed between the articular ends of bones, where they act as buffers, obviating shocks and the effects of great pressure. Examples are found in the temporo-maxillary, sterno-clavicular, perhaps acromio-clavicular, ulno-cuneiform, and some other articulations; also in a modified form in the knee-joint.

(2) *Circumferential* (or *marginal*). These structures are attached around the margins of articular surfaces, and deepen the enclosed cavities. They are exemplified in the cotyloid and glenoid ligaments, of hip and shoulder-joints respectively.

(3) *Connecting* fibro-cartilages bind firmly together the adjacent surfaces of bones, and are found intervening between the bodies of the vertebræ, in the symphysis pubis, &c.

(4) *Sesamoid* fibro-cartilages are found in the substance of certain tendons in situations where the latter play over a bony surface. Examples are found in the tendons of tibialis anticus, tibialis posticus, peronæus longus, outer head of gastrocnemius, flexor brevis pollicis (manus and pedis) in both tendons.

Reticular Cartilage.—This tissue is known also by the names of *elastic*, *yellow fibro*, or *spongy* cartilage. It is flexible

and elastic, and does not tend to ossify. Its matrix is formed elastic fibres; and in the meshwork formed by these are imbedded cartilage cells. The latter are numerous, and in thin sections they readily drop out, leaving a reticular matrix.

This variety of cartilage is found in the epiglottis, cornicula laryngis, cuneiform cartilages of larynx, in the cartilage of the Eustachian tube, and in that of the pinna.

(4) *Osseous tissue*.—Of bony structures there are two varieties, the *compact* and the *cancellous* (or *spongy*). On microscopic examination, however, it will be found that there is no essential difference between the structure of the two, excepting that the open spaces which exist in each are much wider in the latter. The compact tissue forms nearly the whole of the shafts of the long bones, and also a thin encrusting layer around the articular ends of these as well as around the cancellous structure of the long and flat bones.

On examining a section of osseous tissue under the microscope it is found to be perforated by numerous small apertures named the *Haversian canals*, the average diameter of which is about $\frac{1}{100}$ of an inch (varying from $\frac{1}{200}$ to $\frac{1}{50}$). They diminish in width towards the circumference of the bone. These canals lodge the blood-vessels in the recent state. They are surrounded by a series (4-15) of concentric rings (*lamellæ*), which are seldom quite circular, and which are, in addition, perforated by minute pores (*canaliculi*) which communicate with larger spaces (*lacunæ*) lying between the adjacent lamellæ. The lamellar rings are not all complete, some ending between the others. The lacunæ lodge the bone-corpuscles which also send processes along the canaliculi to meet with similar ones from the neighboring corpuscles. The bone-corpuscles and their processes do not completely fill the spaces which they occupy, but leave room for the plasma to trickle around, and so convey the nutritive material to the osseous tissue. Besides those which surround the Haversian canals there are other (so-called *circumferential*) lamellæ, which are arranged concentrically with the surface of the bone, and are placed, some near the surface, and some between the Haversian systems in the interior. There are also lamellæ found here and there, which are irregularly disposed with regard to the others (*interstitial* or *ground lamellæ*). Between the Haversian systems there are irregularly shaped *Haversian spaces*, produced by absorption of the

osseous tissue. This mode of formation is indicated by their eroded outline, and by their encroaching in some places

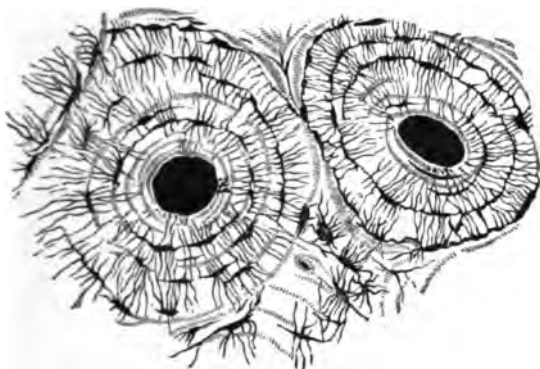


Fig. 32.

Transverse section of compact bone, showing two Haversian systems. Each presents the central canal, with the surrounding lamellæ, lacunæ, and canaliculi.

on the lamellæ of the adjacent Haversian systems. Beneath the articular cartilage is found a dense layer (*articular lamella* of Toynebee), which has no Haversian canals, as it is not perforated by the blood-vessels. The capillaries turn back in loops on approaching it, and the articular lamella itself contains a much larger proportion of the earthy salts than the ordinary bony tissue.

In a piece of bone which has been softened by steeping in a dilute acid solution, thin layers may be peeled off longitudinally, each of which is found on examination to consist of several lamellæ. These lamellæ are found to be perforated with minute openings at short distances apart, and which appear to correspond to the course of the canaliculi. Also on separating the lamellæ *perforating fibres* (first described by Sharpey) may be found passing through several layers, and, as it were, bolting them together. They are continuous with the periosteum on the outside (Kölliker). According to some histologists (Rouget, Neumann, &c.), the proper wall of the lacuna and its canaliculi may be detached with the included bone-corpuscle after decalcification. If the thinnest part of a detached longitudinal

film from the surface of a decalcified bone be examined microscopically, the lamellæ are found to be formed by extremely fine fibres interlacing at very acute angles, so as to form an excessively fine meshwork.

A longitudinal section of a long bone presents appearances in accordance with the arrangement of the Haversian systems above described; the Haversian canals passing vertically and communicating through the lamellæ with the neighboring lacunæ. In the centre of the shaft of each long bone is the so-called medullary canal, which contains the medulla or marrow. It is lined by a thin layer of membrane, the *endosteum*, while the outer surface is covered by a well-defined membrane, the *periosteum*. Several mechanical advantages are gained by the hollow formation of the long bones; they are stronger in proportion to their weight, and lighter in proportion to their strength, than if solid throughout. They are also much more elastic; fractures would be far more common if bones were solid, and the usual formation gives a more extensive surface for muscular attachments.

The *periosteum*, or investing fibrous membrane of bone, covers every part of the non-cartilaginous surface. It is composed of two layers: (a) an external, made up of a meshwork of white fibres, with connective-tissue corpuscles in the interfascicular spaces; (b) an internal or *osteogenetic* layer, which is much more vascular, and contains more numerous cells, enclosed in a delicate reticulum of connective-tissue fibrils. In growing bone a layer of flattened cells may be found, covering the young lamellæ beneath the periosteum; these are the *osteoblasts* of Gegenbaur.

Of the *marrow* which fills the medullary canal and other cavities of bone there are two varieties, the *yellow* and the *red*. Both are very vascular, the vessels being distinguished by the thinness of their walls. The yellow marrow is chiefly formed of fat cells, and passing between them are membranes of flattened corpuscles, and variable numbers of round, oval, or polyhedral corpuscles. The latter are the *proper marrow cells* of Kölliker; they resemble lymph-corpuscles as regards size and aspect. These cells make up the bulk of the *red* marrow, which is the vascular substance that fills the meshes of spongy osseous tissue, and contains few fat cells. Peculiar cells have also been observed in the red marrow, the size of which is

somewhat greater than that of a red blood corpuscle, and the color a similar uniform yellowish-green. They are probably transitional forms between marrow-cells and colored blood-corpuscles (Neumann, Bizzozero).

Among the marrow-cells, especially in the red marrow, multinuclear giant cells (*myeloplaxes* of Robin) are conspicuously seen. They are most numerous near the osseous tissue.

The yellow marrow contains about 96 per cent. of fat; of the remaining four parts, one is formed by connective tissue and the other three by water.

Bone is well supplied with *blood-vessels*, of which it receives three sets. A moderately large *nutrient artery* enters the shaft of the bone for the supply of the contents of the medullary canal; minute twigs from the periosteal membrane enter the bone at all points of the surface covered by this membrane, while a few branches of intermediate size enter the extremities of the shaft at the margins of the articular surfaces. The arteries and veins occupy separate Haversian canals, according to Todd and Bowmann; the veins have extremely thin coats, and present, at irregular intervals, pouch-like dilatations.

The *lymphatics* of bone are not very well known, but the course of some have been described and figured by Mascagni and Cruikshank. They accompany the blood-vessels.

The *nerves* of bone are scanty, and healthy bone seems to be hardly at all sensible to pain; but when inflamed, or otherwise diseased, it may be acutely sensitive.

Growth of Bone.—Bones are developed in one of two tissues, cartilage or membrane.

Examples of *intra-membranous* ossification are found in the tubular bones of the skull. If the membrane be examined in the early stage of the osseous formation it is found to present the structures characteristic of periosteum, and consists of an outer fibrous and an inner osteogenetic layer, the latter part presenting among the blood-vessels large nucleated cells (*osteoblasts*). When ossification commences these cells increase rapidly in number, and form groups. The outer layer of these cells forms the osseous substance, while the inner part remains as the *bone corpuscles* deposited in the *lacunæ*. The groups or rows of osteoblasts in this way produce a meshwork of bony trabeculæ, the interstices of which are filled by these cells, and

are gradually diminishing in size from the new formation of bone around. The process of bone formation proceeds from the deeper part of the membrane, where the *centres of ossification* appear, to the periphery.

As the growth proceeds portions of the young trabeculae become absorbed (*osteoporosis* of Schwalbe); and in the Haversian spaces so formed concentric lamellæ of osseous tissue are deposited, leaving the Haversian canal in the centre.



Fig. 33.

Section of ossifying cartilage.—a, b, two of the young osseous processes, with a few degenerating cartilage-cells; at c, c, the arrangement of the cartilage-cells near the ossifying tissue is shown.

The long and irregular bones are developed by *intra-cartilaginous* ossification. The form of the future bone is represented by a mass of solid hyaline cartilage invested by perichondrium, and very rich in cells, deposited, without any definite order, within a pellucid matrix. Where ossification is about to commence the cells are found to be larger, and placed with their long axis across the shaft of the bone. They then proceed to form vertical columns, between which the matrix forms clear longitudinal lines, intersecting at very acute angles. These soon become the seat of the osseous deposit. The perichondrium, at this early date, consists of two layers, an external and an internal; the latter is the osteogenetic part, and sends processes of various lengths into the cartilage-substance (*periosteal processes* of Virchow). This layer possesses numerous spherical cells (future osteoblasts), while the outer layer presents the ordinary appearances of embryonic connective tissue.

The cartilage channels which hold the periosteal processes form a network of anastomosing tubes, containing a vascular

tissue, crowded with cells, and continuous with the internal layer of the perichondrium (periosteum). The lacunæ of the cartilage cells which lie next these canals now become larger, and soon open into the lumen of the latter, the cartilage cells undergoing disintegration. Instead of the smooth cartilage canals formerly existing, "we now find in these places irregular cavities, into which projects a network of trabeculæ of calcified cartilage" (Klein). These *primary marrow cavities* are still filled with the periosteal processes which expand to fill them, and now receive the name of *primary marrow*. The cells of the superficial part of this marrow are found arranged on the surface of the calcified trabeculæ, and they rapidly form true osseous tissue, which then ensheaths the calcified trabeculæ. The latter gradually undergo absorption, and finally the calcified cartilage tissue will be found to have disappeared altogether, and the trabeculæ formed of true osseous tissue; not, however, presenting a lamellar structure, but forming a peculiar trellis-work (v. Ebner).

The so-formed endochondral spongy bone then undergoes absorption; the process beginning in the centre and proceeding outwards till it at last disappears completely, leaving a large *central marrow cavity* filled with marrow. Concurrent with the process of absorption of the endochondral bone is the formation of periosteal bone, which surrounds the former, and grows from without inwards to replace it. The osteoblasts of the inner layer of the periosteum rapidly proliferate and form processes of cells which, growing inwards, form a network, that is soon replaced by osseous tissue. The osteoblasts in this, as in case of intermembranous bone, seem to form both the osseous matrix and the bone corpuscles (Gegenbaur, Waldeyer); the outer portion of the cell forms the osseous matrix, while the inner remains as the nucleated bone-corpuscle (Waldeyer). The bone-cell and its containing space become branched, and the cells with their processes come to occupy the lacunæ and their canaliculi, as in adult bone. New layers of osteoblasts form on the surface of the trabeculæ, and in their turn form new layers of osseous substance. This goes on till the whole of the tissue of the shaft is derived from the periosteum. The trabeculæ then undergo partial absorption, the spaces in this way becoming enlarged (*osteoporosis*). In the resulting *Haversian spaces*, concentric lamellæ are then laid down from without

inwards, leaving the Haversian canals in the centre. This process of osteoporosis and the formation of Haversian systems do not take place in the superficial part of the bone.

Of the further growth of bone the increase in girth takes place by circumferential deposit beneath the periosteum, while the medullary canal undergoes simultaneous enlargement from absorption. In Duhamel's famous experiment of placing a ring on the wing-bone of a growing pigeon, it was found that it became gradually covered by new bone from without, while the inclosed layers of osseous tissue grew thinner, till at last the ring lay free within the enlarged medullary canal. The fact that madder, added to the food of an animal, stains growing bone, has also been utilised for the purpose of demonstrating the seat of deposition of new osseous tissue, and the same results have appeared.

The process of absorption is continually taking place during the life of bone. According to the researches of Loven, Kölliker, and others, the process is dependent on the presence of large multi-nuclear cells (*osteoclasts* of Kölliker, *myeloplaxes* of Robin). They lie in the marrow cavities and Haversian spaces, and excavate, in the parts with which they are in contact, small shallow pits in which they lie (*lacunæ* of Howship). The osteoclasts are generally more opaque on the side in contact with the osseous substance which is about to undergo absorption, and present in this situation a thick striated border, somewhat similar to the basilar border of the columnar cells of the alimentary mucous membrane. These cells seem to be derived from the osteoblasts, and do not seem to be in every case associated with the process of absorption; indeed, "there are other places where they can be shown to be concerned in the formation of osseous substance, just like the ordinary uni-nuclear osteoblasts" (Klein).

MUSCULAR TISSUE.

The phenomenon of contractility which can be seen in various cells, such as the pale blood-corpuscles, the connective-tissue corpuscles, &c., is displayed in its highest perfection in muscular tissue. Of this important tissue, on the functional activity of which all the active movements of the body depend, there are two varieties—the *striated* (striped) and the *non-striated*

(unstriated). They are also distinguished as the *voluntary* and *involuntary* respectively, from the fact that the former is directly under the control of the will, and the latter not. Striated muscular fibre is, however, found in organs whose functions are not influenced by the will, such as the heart, gullet, &c.

Striated muscular fibres form the voluntary muscles throughout the body. They present the highest degree of perfection of contractile substance.

A voluntary muscle is enclosed in a fascial sheath (*perimysium*), which sends in processes from its deep surface to enclose bundles of the primitive fibres. These bundles are

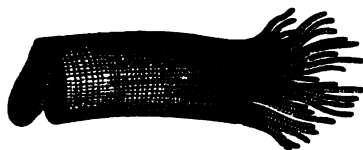


Fig. 34.

Striated muscle fibre, showing the separation into transverse discs at one end, and the separation into longitudinal fibrillae at the other (after Todd and Bowman).

called *fasciculi* or *funiculi*, and the investing sheath of each is known as *endomysium*. The individual primitive fibres which form these fasciculi are found on isolation to be each about an inch and a-half in length (Herzig, Krause, &c.), of cylindrical form, and tapering to either end. Each was developed in early embryonic life from a single spindle-shaped cell (Remak, Kölliker). It is enveloped by an elastic membrane (*sarcolemma*, *myolemma*), which presents on its deep surface oval flattened nuclei, longitudinally arranged (*muscle corpuscles* of Max Schultze).

When a perfectly fresh fibre is examined under the microscope, it presents transverse striations, alternately light and dark in color, and in some cases longitudinal striæ, less well pronounced, are also discernible. (In those animals, such as the rabbit, in which the voluntary muscles are divisible into the red and pale, the longitudinal striations are very distinct in the former, but hardly noticeable in the latter.) If such a fibre be treated with dilute hydrochloric acid, it is separated into horizontal discs; if acted on by alcohol, osmic acid or potassium bichromate it splits up into longitudinal *fibrillae*. These fibrils are specially developed and easily separated in certain insects, &c., and appear to be formed of dark-colored and light segments alternately superposed. Some authors, and

especially Bowman, basing their views on this appearance, have regarded muscular fibre as being made up of a semi-fluid substance, having solid elements (*sarcons elements* of Bowman, *muscle-prisms* of Krause) regularly arranged within it.

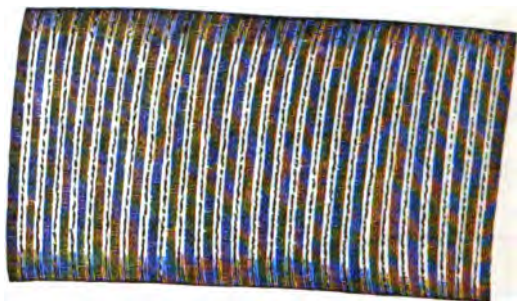


Fig. 35.

A portion of a muscle-fibre (human) magnified nearly 800 diameters
(from Quain's Anatomy, 8th ed.).

The transverse striations of human muscle, which are alone visible while the specimen is fresh, present the appearance of alternate light and dark bands of equal depth ($\frac{1}{1700}$ of an inch). The light band is seen to be crossed by a row of dots (the *dotted line* of Busk and Huxley, *granular layer* of Flögel), whose appearance has been explained in various ways by different observers. The dark band is somewhat lighter in color along the centre, the brighter part not forming a continuous line. According to Brücke, the dark segments of muscle fibre are *anisotropic*, and possessed of double refraction; while the light-colored bands are *isotropic*, and possessed of single refraction only.

Brücke's results have, however, been questioned by Rouget, Ranvier, and other observers.

Recent researches, made with the aid of very high magnifying powers, show the intimate structure of muscle fibre to be much more complex. The anisotropic band (A) is shown to be completely divided into two transverse segments. (*Querscheiben*) by a light-colored one, the *median disc* (*Mittelschreibe*) of Hensen (1); the isotropic segment (I) is divided by a dark trans-

verse band, the *disc of Krause*, which is in turn divided into five secondary striæ; a median (3), dark in color, the *intermediary disc* (*Zwischenscheibe*) of Engelmann, (*terminal disc of Merkel*), which is separated by two clear bands of isotropic substance from the narrow striæ (4), a little less dark in color, that limit the median disc, the *accessory discs* (*Nebenscheibe*) of Engelmann. The intermediary disc is very elastic, possessed of double refracting power, and is firmly united to the sarcolemma.

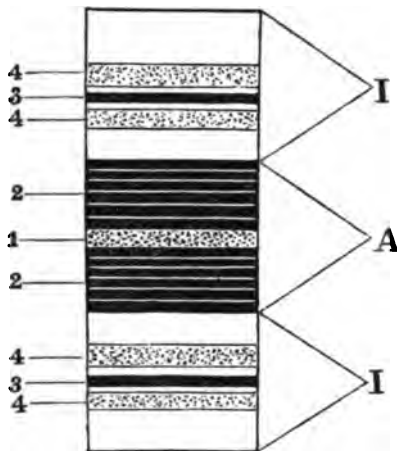


Fig. 36. (After Engelmann.)

Longitudinal membranous partitions are described by Krause, Merkel and others, which divide the space between two intermediary discs (*muskelfach*) into what Krause calls *muscle-caskets* (*muskelskästchen*), each of which is filled, according to him, by a solid body (*muscle-prism*) surrounded by a fluid. According to

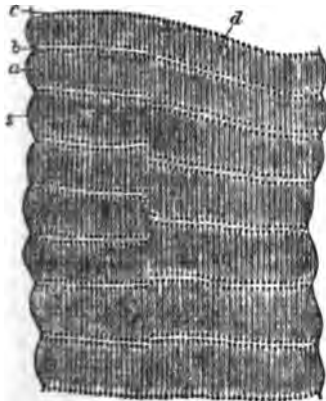


Fig. 37.

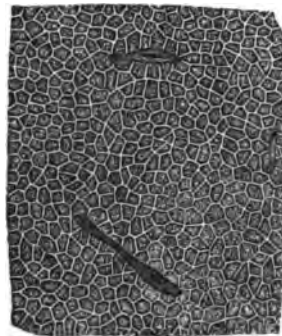


Fig. 38.

Rouget, each muscle fibril is formed by the turns of a ribbon-shaped band, coiled in a spiral form; the intervals between the turns forming the light striæ, while the dark correspond to the spiral band itself. According to Schäfer, muscle fibre (see Fig. 37) is made up of a "homogeneous ground-substance, in which lie imbedded successive series of *rod-shaped particles*, the enlarged ends of which give the appearance of transverse lines of dots, and by diffraction produce a relatively bright appearance in their immediate neighborhood, and, therefore, give rise to the bright bands." The constituent fibrils are united by an interstitial substance which, in transverse sections (Fig. 38) hardened by chromic acid, presents the appearance of polygonal compartments, bounded by well-defined lines (*Cohnheim's areas*).

The nuclei (*muscle corpuscles* of Max Schultze) which are found on the deep surface of the sarcolemma, have been already mentioned. In some mammals they are also found in the deep part of the muscle tissue.

The surrounding sarcolemma may be demonstrated by placing in water which, by imbibition, lifts up the membrane from the surface of the enclosed fibre; or merely by tearing the muscle, when the sarcolemma of some fibres will be found to remain unbroken after the enclosed tissue has given way.

According to many authorities, the contractile part of muscle fibre is also in a fluid or semi-fluid state during life, and Kühne, who has seen a parasite (*Myoryctes Weismanni*) move within the substance of living muscle, strongly advocates this view. Numerous powerful objections have, however, been raised against this idea.

Ranvier has called attention to the *spectrum* of striated muscle fibre, and devised an instrument (*myospectroscope*) for the examination. It resembles that of hæmoglobin.

The *blood-vessels* are very numerous, and the capillaries run parallel to the fibres and form a network, with rectangular spaces. The arrangement is such that every fibre is in contact with at least two, and sometimes with four or five capillaries. Of the *lymphatics* little is known, but they have been demonstrated by Sappey, George and Francis Hoggan (diaphragm), His and Belajew (heart).

Muscle is freely supplied with *nerves*; but the richness of the distribution varies with the functional activity. In the

ocular muscles a nerve-fibre supplies 3-10 muscle fibres; in such muscles as the sartorius, one fibre is distributed to no less than 40-80 muscle fibres. On coming into proximity with the muscle fibre to which it is distributed, the sheath of Schwann (or, according to Ranvier, the sheath of Henle) becomes continuous with the sarcolemma, the nerve fibre loses the medullary sheath, and the axis cylinder seems to expand, forming a broad granular mass of oval outline, which is freely supplied with nuclei. This is the nerve-eminence (*Nervenbügel*) of Doyère; it contains the translucent non-granular substance, which encloses the termination of the nerve-fibre. The latter portion is known as the *motorial end-plate* (*plaque motrice terminale* of Rouget, *motorischen Nervenplatte* of Kühne). On examining with very high magnifying powers, it will be found that the granular mass encloses, but is not formed by, the branching network formed by the fibrillæ of the axis-cylinder (*arborisation terminale* of Ranvier). These fibrils have small irregular nuclei here and there, while the enclosing granular mass (*substance fondamentale*) presents large, oval nuclei (*noyaux fondamentaux*) placed in contact with the contractile substance.

Sensory nerve-fibres distributed to striated muscle have been described by Külliker, Reichert, and others. The fibres so regarded have no medullary sheath. Tschiriew has observed those fibres, but affirms that they do not terminate in the muscle itself, but merely pass through to be distributed on the aponeurotic sheath.

Chemical composition.—Striated muscle fibre is composed (chemically) of two parts: (1) the muscular substance, properly so-called; and (2) the insoluble residue formed by the sarcolemma, muscle-corpuscles, and a little fatty matter.

The *sarcolemma* presents most of the characters of an elastic membrane, but is more readily acted on by chemical re-agents. The muscular substance (*muscle-plasma* of Kühne) may be obtained by freezing a piece of muscle immediately after removal from the body, and, while frozen, mincing and rubbing it up with snow containing one per cent. of sodium chloride; a mixture is obtained which at a temperature just below 0°C. slowly filters. The filtrate is the muscle plasma. It forms an opalescent fluid of syrupy consistence, with a slightly yellowish tinge, and alkaline reaction. It coagulates spontaneously at the ordinary temperatures, forming a clot composed of a special

substance (*myosin* of Kühne), and a fluid, *muscle-serum*, or *muscle-juice*.

Myosin is a colorless substance, neutral in reaction, insoluble in water, but soluble in dilute solutions of sodium chloride (5-10 per cent. The solutions do not coagulate spontaneously; but heat, alcohol, concentrated solution of sodium chloride (10-20 per cent.), or an excess of water, precipitates myosin in the form of coagulated albumin. It decomposes peroxide of hydrogen, and is changed by acids into acid-albumin or syntonin.

Muscle serum contains the following matters:—

(1) *Albuminoids*: (a) a potassium albuminate, precipitable by acetic acid; (b) an albumin coagulable at 45° C. (113° F.), and insoluble in saline solutions; (c) a considerable proportion of an albumin coagulable at 75° C. (167° F.).

(2) Traces of *ferments*; pepsin (Brücke), and ptyalin (Piotrowsky).

(3) *Peptones*.

(4) A *coloring matter* identical with that of the blood, and which remains after all the blood has been removed by washing out the vessels; it also exists in certain animals whose blood contains no hæmoglobin.

(5) *Nitrogenous principles*: creatin, xanthin, hypoxanthin, inosic acid, uric acid, &c. Creatinin has been sometimes found, but does not appear to be a normal constituent.

(6) *Non-nitrogenous principles*; fat, inosit, another and distinct kind of sugar, has been described by Meissner; glycogen (especially in the muscle of the foetus; glucose (probably formed from the glycogen) by the influence of the saccharifying ferment mentioned above; paralactic (or sarcolactic) acid, which is isomeric with the lactic acid of fermentation, and a small quantity of ethylenic lactic acid, which probably does not form till after death; fatty acids, formic and acetic, of which the existence during life is doubtful.

(7) *Salts*, among which the acids, phosphates, and potash salts predominate, as they do in blood-corpuscles (the preponderance of potash over soda being still more marked than in the latter); carbonate of lime, magnesia, iron, chlorine, sulphuric acid. The ash of muscle tissue is acid.

(8) *Water*, which forms three-fourths of the weight of muscle. The maximum proportion exists in cardiac muscle; it is greater

in the female than in the male, and greater in the foetus than in after life.

(9) *Gases*, of which carbonic acid forms the largest proportion (14.40 per 100) ; a little nitrogen (4.9 per 100) ; and traces of oxygen (Szumonski).

The following analysis of the muscular tissue of mammals is after K. B. Hoffmann :—

Water (per 1000)	. 745—783	Taurin	.7 (horse)
Solids	. 217—255	Inosit	.03
Organic matters . .	. 208—245	Glycogen	4.1—5
Inorganic	. 9—10	Lactic acid	.4— .7
Coagulated albumin, sarcolemma, &c. . .	. 145—167	Phosphoric acid . .	3.4—4.8
Albuminate of potash .	28.5—30.1	Potash	3.0—3.9
Creatin	. 2	Soda	.4— .41
Sarcin	.2	Carbonate of lime . .	.16— .18
Xanthin & hypoxanthin	.2	Magnesia	.4— .43
Inosate of baryta . .	.1	Chloride of potash . .	.04— .1
		Oxide of iron	.03— .1

Consistence—The consistence of muscular tissue varies with its condition. When stretched by the ends it is tense and hard, when not stretched it is soft, and semi-fluctuating whether at rest or contracted ; it is the tension of the extremities that alone determines the hardness of muscle. During rigor mortis the hardness of muscle attains its maximum.

Cohesion—The cohesion of muscular tissue is much less than that of the connective-tissues, especially of tendons. It is chiefly due to the sarcolemma, with the connective-tissue and vessels entering into its structure ; and it is markedly less in the muscles of which the sarcolemma is very delicate, as in the tongue.

Elasticity.—The elasticity of muscle fibre is very perfect, if feeble. The elongation produced by attachment of a weight to the end of a piece of muscle is not exactly proportional to the weight attached ; and, as the weights increase, the curve of the muscular elasticity is found to approach that of an hyperbola (Wertheim). According to Wundt, a weight of 273.4 grammes doubles the length of a square millimetre of the transverse section of a muscle. The limit of elasticity is easily surpassed : the gastrocnemius of a frog, if charged with a weight of 100 grms., does not return to its original length. According to Weber, a muscle during contraction is less elastic, and more

extensile. This accounts for the result of a curious experiment of Weber : if a considerable weight be attached to a muscle in repose, when a stimulus is applied the muscle will be found to become elongated instead of contracting ; this is due to the fact that the shortening caused by the contraction is not sufficient to compensate for the lengthening due to the diminution of elasticity. The results of Weber have, however, been disputed by Volkmann, and Wundt has arrived at directly opposite conclusions.

Tonicity.—The muscular tonicity is but a special form of elasticity. In the living body the muscles are hardly ever of their natural length ; they are *stretched* between their points of attachment, and this tension is maintained by the elasticity of the surrounding tissues, both hard and soft, and also by the antagonism of neighboring muscles. The tonicity of muscle fibre seems to be influenced by the nervous system. If the spinal cord of a frog be divided below the medulla oblongata, and then the nerves of the hind limb on one side, when the animal is suspended by the head the articulations of the corresponding limb will be found to be more relaxed and less flexed than on the opposite side (Brondgeest). This would seem to shew that the muscles were furnished by the spinal cord with a peculiar nervous influence which maintains a slight degree of permanent contraction. The question of muscular tonicity has recently entered a new phase in connection with the phenomenon of *tendon-reflex*. On sharply striking the ligamentum patellæ, or sudden stretching of this structure, a rapid movement of extension of the leg follows. This movement was supposed by Westphal to be due to mechanical stimulation of the quadriceps by the shock to the tendon, but this idea is disproved by the fact that the fibres contract simultaneously along the whole length of the muscle ; the contraction does not commence at the lower end, and no muscular wave is developed, as occurs in cases of contraction following direct mechanical stimulation. It is a true reflex contraction, and experiments on the lower animals show that the stimulation does not proceed from the skin, but from the tendon itself, and probably from the nerve filaments distributed to the aponeurotic muscle-sheaths. These musculo-tendinous sensory fibres must be very sensitive, for very slight stretching of the anterior crural nerve destroys the tendon-reflex, while

voluntary motion, reflex cutaneous irritability, and faradic irritability remain intact (Westphal). The tendon-reflex is destroyed in the rabbit by section of the posterior roots of the lumbar nerves, and destruction of the corresponding part of the spinal cord (Tschiriew).

Nutrition.—The nutrition of muscular tissue is extremely active. Muscle, even when deprived of blood and completely at rest, absorbs oxygen and eliminates carbonic acid, in slightly smaller quantity, or, in other words, it is the seat of a veritable respiration. The elimination of carbonic acid persists, although in diminished quantity, even when the muscle is placed in hydrogen or in nitrogen. The respiratory process is more active in muscle than in any other tissue, and is less active in cold-blooded or in new-born animals than under the opposite circumstances.

The chemical phenomena which take place in muscle during repose are influenced, to some degree at least, by the nervous system. Muscular metamorphosis has been found to diminish after section of the corresponding nerves, or after they have been paralysed by curara or morphia (Rührig, Pflüger, &c.). This nervous influence has received from some physiologists the name of *chemical tonus* (*tonus chimique*) of muscle. It is of reflex nature, and dependent on the influence of the stimuli applied to the sensory nerves, and, accordingly, the activity of the nutritive phenomena of muscle is increased by cold, light, irritation of cutaneous nerves, &c., and diminished under the opposite conditions. On this account there is a marked difference between a muscle which is simply inactive, and a muscle which has been paralysed by division of its nerve. Disturbance of the nerve accordingly leads to structural changes in muscle, atrophy, fatty degeneration, &c. These changes are not due to vaso-motor influence, as was at one time supposed by some, for it does not follow similar lesions of the sympathetic nerves or ganglia. It has been suggested by Brown-Sequard and Charcot that the muscular lesions were due to irritation of the nerve fibres produced by the section; but this theory is not supported by the results of Vulpian's experiments, who found that the changes were not more rapid after incomplete section, or irritation of the nerve-trunk, than after complete and careful division. By exclusion then we are led to believe that the nerve centres exercise some peculiar influence on the nutritive

changes which go on in the muscle, the suppression of which gives rise to troubles in its growth and metamorphosis.

Muscular tissue is very rich in *blood-vessels*. The muscular system of the rabbit contains, according to Ranke, 20.2 per cent. of the whole blood of the body. The vessels seem to be supplied, like other blood-vessels elsewhere, with vaso-constrictor and vaso-dilator nerves. The vaso-dilator element seems, however, to predominate; for, on stimulation of a muscular nerve, an increased flow of blood towards the muscle is observed to take place simultaneously with the contraction. This vascular dilation has been observed directly, by the aid of the microscope, on the hyoglossus of the frog, and it has been seen to take place even after removal of the heart or deligation of the aorta (Gaskell).

Irritability and Contractility.—The irritability of muscular tissue is the peculiar property which it presents of contracting under the influence of external stimulation. It was first specially recognised by Haller, and as it causes the peculiar movement of shortening, it has been called *contractility*, which is a preferable appellation, as irritability is a property of all living tissues.

Whether this property depends on the nerves distributed to muscle, or is inherent in the muscular tissue itself, is a point which has given rise to a great deal of controversy, but the latter view is probably the correct one, for the following reasons:—(1) Muscular tissue is but a form of contractile protoplasm; and although very highly developed, its movements resemble those of the latter substance, which are proper to itself and entirely independent of nervous influence. (2) When the muscular nerves have been destroyed or paralysed the muscle-tissue still preserves its contractility. This is shown in several ways, as by division of the nerves, by the action of curara, or by the influence of a constant ascending current. The action of curara has been a great deal disputed; the objection was made by Funke that the axis-cylinder of the nerve fibre was not affected, and by Kühne that the irritation of the muscle diminished from the point of entrance of the nerve towards the extremities; and the latter accordingly agreed that a special nervous apparatus existed in the muscle which escaped the action of the poison. This, however, has been shown by Sachs to be a mistake; when the curarisation is

complete, the irritability of all parts of the muscle is equal. Both the medullated and non-medullated nerve fibres resist the action of curara, and its influence seems to be confined to the motorial end-plates.

When an ascending constant current is passed into a motor nerve (anelectrotonus) the latter loses its irritability, and no longer causes contraction of the muscle on stimulation; but contraction may still be called forth by direct stimulation. The irritability is certainly diminished; but this is satisfactorily explained by Pflüger, who observes that on direct stimulation, while the nerves are intact, both nerve and muscle are irritated, but the latter only when the nerves have been previously paralysed.

(3) Contractility exists in muscles, or in portions of muscles entirely void of nerves. This has been demonstrated in the case of some muscles which contain no nerve-fibres in a part of their course: sartorius of frog (Kühne), retractor bulbi oculi of cat (Krause), &c.

(4) Certain agents act on muscle-tissue without affecting the nerves; and inversely, according to Kühne, certain chemical agents (ammonia, lime water, very dilute acid solutions) have no action on the nerves, but when applied directly to muscle (whether intact, or paralysed by curarisation or nerve-section) they produce contractions. These results have, however, been attacked by Wundt, Funke, and others.

(5) The phenomenon of the so-called *idio-muscular contraction* also supports this view. Bennett-Dowler observed the production of muscular contraction after death on the application of a mechanical stimulus. Since then it has been studied with great care by Brown-Sequard, Schiff, Auerbach, &c., and has been also observed in cases of decapitated criminals, and in amputated limbs. The special form of contraction, which has been named *idio-muscular*, is the local one, which gives rise to the formation of a ridge at the point irritated or struck; the latter either remains confined to the spot, or forms the origin of two waves, which proceed to either end of the muscle, which then return to the original starting-point. The extreme-muscular irritability of phthisical patients (pointed out by Stokes) exemplifies this form of contraction (*myoidema* of Lawson Tait).

The irritability of muscle is increased by: vascular dilation, rest, presence of oxygen, heat (up to a certain point), veratrin, eserine, &c. The passage of a constant galvanic current along

the length of the fibres has the same effect. Irritability is retained longer in oxygen than in air, and longer in air than in a medium containing no oxygen; the injection of oxygenated blood into the vessels of an amputated limb maintains the irritability of its muscle for a considerable time. The opposite conditions have the contrary effect: arrest of the arterial circulation as by ligature or compression of the aorta (Steno's experiment), fatigue, rest (when too long maintained), a temperature much above or below the medium, forcible extension, or the presence of certain substances in the muscle, such as carbonic acid, lactic acid, phosphate of lime, and certain toxic substances, such as digitalin. Some poisons destroy the irritability of muscular fibre almost instantaneously, such as the sulphocyanide of potassium (and other potash salts), bile, emetin, saponin, upas antiar, &c.

Section and paralysis of nerves are followed by peculiar modifications of the muscular irritability. On the third or fourth day, a diminution of irritability is observed for stimulation direct or indirect, of whatever kind it may be. At the end of some weeks, the muscles become more susceptible to mechanical irritation, and the action of continued currents, while they become insensible to currents of short duration, and to induced currents (Erb). The results of Erb have, however, been questioned by Vulpian, who has not found the same increase of excitability for induced currents, nor has he found the difference described by Erb between the paralysed muscles and those whose nervous supply is intact, and he has always, in both kinds of muscles, found the negative pole to act more strongly than the positive, which is the contrary of Erb's experience. To this increase of irritability after division of the nerves must, probably, be attributed the fibrillar contractions which have been observed by Schiff, Bidder, and others after division of the nerves of some muscles (tongue, face, &c.). These paralytic contractions appear about the third day, and last sometimes for several months. They persist after the deligation of the arteries, and are not arrested by curarisation (Bleuler and Lehmann). Muscular contractility is more feeble in newly-born animals than in adults (Soltmann), and the same is true of the muscles of the embryo (Legros and Onimus).

Contractility persists some time after death. In an executed criminal Onimus saw the contractility disappear first in the

muscles of the tongue and diaphragm, then from those of the face (2½—3 hours after death); of the muscles of the limbs the flexors remain longer contractile than do the extensors; the muscles of the trunk, and especially the abdominal muscles, retain their contractility longest. It is retained longer at a low temperature, and even after disappearing may be restored by injection of oxygenated blood into the arteries of the muscle.

Stimuli.—There is no such thing as a spontaneous muscular contraction; it is always called forth by the application of an external stimulus. Even in those cases where careless observation would seem to show that the latter was entirely absent, a more thoughtful consideration will show that some such influence as that of temperature, sudden contact of air, fluid, &c., existed.

For the present we shall confine our remarks to the action of direct stimuli, and these may be divided into mechanical, physical, and chemical.

(1) *Mechanical.*—Every mechanical irritation of a muscle (section, percussion, pricking, &c.), provokes a contraction which becomes persistent when the stimulations succeed each other with sufficient rapidity. Even tetanus of the muscles of the hand has been produced by a rapid succession of extension movements of the forearm (40—60 per second), by means of a special apparatus (*Rood's experiment*).

(2) *Physical.*—*Electricity.*—This resembles so closely its action on the nerves, that the study is best taken up in connection with that of the nervous system. The conductivity of muscular tissues is less than that of nervous. The resistance of muscular tissue to the electric current is three millions of times as great as that of mercury, and one hundred and fifteen millions of times as great as that of copper (Ranke). The resistance is greater when the current is applied transversely to the muscle (4.4—9.2 : 1, Hermann). According to Hermann this greater resistance should be explained by the *internal polarisation* described by Du Bois-Reymond. Besides the resistance due to internal polarisation, Du Bois-Reymond has found in animal tissues a *secondary external resistance*, which takes place chiefly at the point of entrance of the current (*anode*).

Constant Current.—In the normal state, the muscle con-

tracts at the closing and at the opening of the current, and remains relaxed during the whole period of its passage. The contraction of closing is more pronounced than that of the breaking of the current; and the latter may be absent if the current be feeble. It has been shown by Pflüger and Chauveau that the nerve is excited by the closing of the current at the negative pole (*cathode*), and by the breaking at the positive pole (*anode*), and the same law has been demonstrated of muscular tissue by V. Bezold and Engelmann. Aebly disagrees with the conclusions of the latter authorities; he has found that the whole length contracted when the current is strong; but when feeble, the contraction of the extra-polar part of the muscle (part not included between the poles of the battery), does not take place except at the time of closing. Wundt has reported a very slight contraction during the passage of the constant current through perfectly fresh muscle; this shortening is greater for the ascending currents, and, according to v. Bezold is but a tetanic prolongation of that contraction. As in case of nerves, the passage of a constant current increases the irritability of the muscle in the neighborhood of the cathode, but only for the intra-polar segment.

Constant currents produce in muscle, as in fluids, *electrolytic decompositions* which play an essential part in the phenomena of contraction; acids are disengaged at the positive pole, while crystals of creatinin are deposited at the negative pole.

Phenomenon of Porret.—(*Electro-muscular transfusion, cataphoric action*). The experiments of Porret have shown the passage of water (in a closed vessel) towards the negative pole, under the influence of a nerve current. Kühne saw, during the passage of a constant current through a muscle with parallel fibres, that an intense movement of undulation took place at the negative pole, by which the muscle diminished in volume at the anode, and increased at the cathode; on breaking the current, the muscular mass returned quite suddenly to the positive pole. He was disposed to refer this change to a phenomenon analogous to that of Porret, and believed that a real movement of the muscular substance took place, but Du Bois-Reymond looks upon it as a local tetanus. According to Jendrassik the phenomenon described by Kühne consists of two parts: (1) a thickening of the muscle at the negative pole; this he refers to the local tetanus of Du Bois-Reymond; (2)

an undulatory movement confined to the intra-polar part of the muscle, and proceeding from the positive to the negative pole: this movement he explains by variation in the size and form of the vessels, produced by the osmotic currents which form under the influence of the electric stimulus (phenomenon of Forret). He also recognises in that phenomenon a true *internal current* which takes place within the muscular fibre, and which can be observed only with the aid of the microscope; at the moment of the closing contraction the transverse striæ of the muscle approach one another at the poles, and he compares the phenomenon to the movements of solid particles suspended in a fluid under the influence of a constant current, as observed by Jürgensen.

Induced Current.—When an induced current of very short duration is passed through a muscle no contraction follows; and, as a general rule, a weak current produces contraction only at the negative pole, while a strong current is followed by contraction at both poles. There is a marked difference in the results according as the direction of the current is the same as that of the muscular fibres, or transverse to the latter, being much less in this case. According to Sachs this difference would be due to the intra-muscular nerves, on which the action of the nerve-current is similar, for the difference is not observable in case of curarised muscles; this, however, has been contradicted by the more recent researches of Tschiriew, Albrecht, and Meyer. These authorities affirm that muscles contract more easily under the influence of the transverse current. (The rule holds good both for constant and induced currents). If this be true, there is a remarkable difference in this respect between nerves and muscles.

Heat.—According to Adamkiewicz, the conductivity of muscle for heat is .0431 (distilled water being taken as unity). Intense cold causes contraction; so does the plunging of muscles into an indifferent fluid of elevated temperature. Heat produces a true tetanus (40° C. in the frog, 45°—46° in mammals). If a frog be plunged into water at 40° tetanus immediately results, and the animal presents a state of rigidity entirely comparable to the cadaveric rigidity, but which disappears at the end of a certain time.

(3) *Chemical Stimuli.*—Most chemical substances act as stimuli to muscular contraction when applied to its surface.

At the same time they generally impair its integrity. Distilled water, when applied directly to muscle, or injected into the vessels, produces violent contractions, even when the nerves have been paralysed by curara.

Muscular sensibility.—In the normal condition, the ordinary mechanical or chemical irritants produce no pain when applied to muscle. Nevertheless, when very firm pressure is made on muscle, it seems to give rise to a peculiar dull pain. Electricity, on the other hand, gives rise to peculiar sensations in muscle, which grows to intense pain when the current is of sufficient strength (*electro-muscular sensibility* of Duchenne). It is not due, as Remak taught, to stimulation of the cutaneous nerves, for Duchenne produced it by direct stimulation of the great pectoral muscle, when exposed after amputation of the breast. Other examples of muscular sensibility are found in the *cramps* of certain muscles, *uterine pains*, sensation of *muscular fatigue*, &c., &c. In some of these conditions the muscle becomes very sensitive to mechanical irritation; for instance, pressure on fatigued muscles may cause considerable pain. Other sensations which have been referred to muscle are: hunger, nausea, desire to go to stool, the desire to urinate, the ocular sensations which accompany the desire of sleep, the sensations about the buccal cavity which precede the act of yawning, the *besoin de respirer*, the genital sensations which accompany the erection of the penis and ejaculation of semen, &c.

Besides the above-mentioned examples, muscular contraction is accompanied by a sensation which gives us consciousness of the occurrence of their contraction. It is that which has been called *muscular sense* by Sir Charles Bell (Gerdy's *sentiment de l'activité musculaire*).

The *muscular sense* (*conscience musculaire*), is the sensation which we have of the contraction of muscles. But it is necessary to distinguish from it the perception of muscular movement, and also the perception of the intensity of voluntary effort, by which we bring about contraction of the muscles. The latter sensation, as Helmholtz has well shown, may be perfectly well developed in the absence of any muscular contraction.

The muscular sense, properly so-called, which informs us of the contraction of the muscle engaged, estimates the following particulars:—

- (1) The *energy* of the contraction (Weber's *sense of mus-*

cular force), by which we are able to appreciate the weight of objects and the resistance which they offer to muscular exertion.

(2) The *extent* of shortening, or the excursion of movement (movement of precision).

(3) The *rapidity* of the contraction (agility of movement).

(4) The *duration* of the contraction.

(5) The *direction* of the movement: this notion is a complex one, due to the auxiliary aid afforded by tactile and visual sensations.

(6) The *position* of the limbs and of the body (sense of equilibrium): in addition to the sense of muscular contraction, there is often also a sensation of passive tension, as in the dorsal decubitus, &c. It is by this sensation that we are able to tell, even in the dark and without the aid of touch, what is the position our limbs may be in. This is of great importance in standing, walking, and in all movements of precision.

The sensation of *bien-être* (*euphoria*), the peculiar feeling of lightness experienced in the body and limbs during perfectly good health, also appears to be a muscular sensation.

Whether there are sensory nerve-fibres distributed to muscle is still an open question, as we have seen, and three different theories exist on the subject:—

(1) According to some there is no special muscular sensibility; we only are sensible of the quantity of nerve-force sent to muscle, or the intensity of the stimulus which proceeds from the nerve centres; we know the extent of the contraction wished and not of that executed; we are conscious of the intention, but not of the fact. Such is the hypothesis of J. Müller, Ludwig, Bernstein, &c., but it is hardly compatible with the existence of such local sensations as those of cramps, and those of muscular fatigue.

(2) According to some other authorities we do not know that a muscle contracts except by the sensations produced in the adjacent skin or mucous membrane (Schiff, Aubert, &c.); according to them it is a purely tactile sensation. This rule cannot apply to the deep muscles, such as the diaphragm, and Rauber has modified this hypothesis by referring the muscular sensibility to the Pacinian corpuscles. In paralysing the latter by section of the nerves in the interosseous spaces of one of the

limbs of the cat, he observed slowness and uncertainty of movements, abnormal attitudes, and difficulty in walking; these phenomena did not appear when the same wounds were made without section of the nerves. For those muscles in whose neighborhood there are no Pacinian corpuscles, he offers explanations of other dispositions which measure the muscular contraction, and in case of some muscles he adopts the theory of Schiff and Aubert.

(3) Another group of authorities (Arnold, Brown-Sequard, &c.) believe that certain centripetal nerve-fibres exist which pass from the muscles to the nervous centres, and transmit the sensation of the muscular contraction executed. Sachs has seen some nerve-fibres remain intact in muscle, when all the motor-fibres had become degenerated after section of the anterior roots of the nerves. He has also seen, in a frog poisoned by strychnia, the irritation of the central end of the muscular nerve to produce reflex cramps, even after section of the anterior roots of the nerves; and stimulation by ammonia of the section of the sartorius muscle, in the part deprived of nerves, had the same effect; showing that muscular contraction alone is sufficient to excite the sensory muscle nerves.

MUSCULAR CONTRACTION.

Myography.—The application of registering apparatus to the study of muscular contraction has received the name of myography, and the registering apparatus itself is known as the myograph. Of instruments specially devised for the registration of the extent of muscular contraction the earliest is the —

Myograph of Helmholtz.—It consists of a metallic plate, moving round a horizontal pivot, and balanced by a counter-poise. In the midst of this plate the tendon of the muscle is attached by a crotchet, and a balance which can be loaded with weights is fixed there also. At the opposite extremity of the axis of rotation is a writing point which traces the movements of the end of the muscle on a vertical registering cylinder. This instrument has been variously modified by Du Bois-Reymond, Sanders-Ern, Kronecker, &c.

Myograph of Marey (simple).—The chief part of this apparatus is formed by a horizontal metallic plate which moves freely along a vertical rod. This plate supports the axis of a registering lever which moves in a horizontal plane; on this lever a plate slides, which has a button above, to which is attached by a thread the tendon of the muscle to be experimented on (usually gastrocnemius of the frog). On the part which forms the axis of the registering lever is rolled a thread, which passes over a

small pulley, and supports a plate, on which is placed the weight which graduates the work of the contracting muscle.

Marey's double or comparative Myograph.—In this instrument there are two levers placed close to one another, so that the tracings can be readily compared; in all other respects it is identical with the one just described. It is used for the purpose of comparing muscular contractions modified by different circumstances (heat, cold, &c.).

Marey's transmission Myograph.—This instrument inscribes the muscular curves with the intervention of a *tambour à levier*, of which the use has been so widely adapted by Marey. The tendon of the gastrocnemius is bound to the lever of one tambour, which communicates with the inscribing tambour in such a way that each contraction of the muscle, by pressing the lever against the membrane of the first, expels a certain quantity of air into the inscribing tambour. In this the movements may be registered at a distance, and the animal may be placed in various positions more easily than when using the simple myograph.

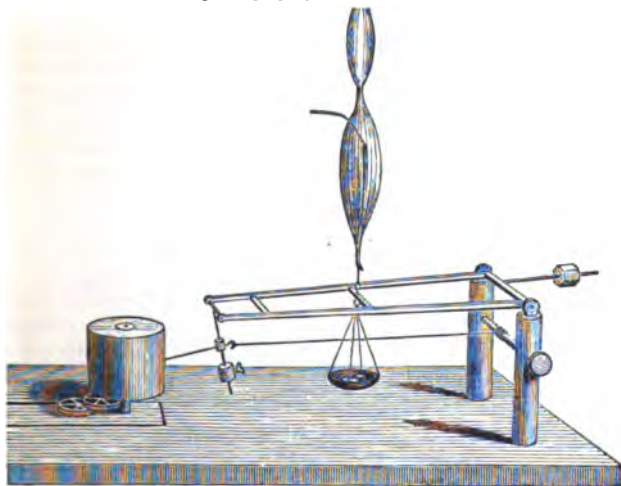


Fig. 39.
Myograph of Helmholtz.

The amount of thickening which the muscle undergoes has also been registered:

The lever of an exploring tambour is armed with a button, which is made to press on the muscle. The movements of the button are then transmitted to a registering apparatus, by the intervention of the tambour in the ordinary way.

Marey's pince Myographique.—This consists of two branches articulated in the centre. At the end, each branch terminates by a metallic disc.

They communicate with the poles of a battery, and embrace the muscle to be experimented on. At the opposite extremity, one supports one of Marey's tambours, and the other moves a vertical rod. When the muscle contracts, it separates the two ends which embrace it; the other two are approximated, the rod presses on the tambour, and the pressure is transmitted by means of a tube to a second tambour, which is connected with a registering apparatus. He has also modified the instrument so as to be applicable to man.

Nasse's Comparative Myograph.—D. Nasse has devised an instrument for measuring the comparative force of two muscles. It consists of a half ring of metal, to which a weight is attached, and which is supported by a pulley of which the axis occupies the long diameter, and over which a cord passes, of which the two extremities are attached to the two muscles whose power it is sought to compare. One of the ends of the axis of the pulley bears a needle, which is placed opposite a graduated circle. When the muscles contract with equal force, the pulley remains motionless, and the needle at 0° ; when the muscle is stronger, the pulley turns, and the needle indicates the difference of power.

The *Antagonistograph* of Rollett is constructed on the same principle.

Under the name of *telegraphe musculaire*, Du Bois-Reymond has described an instrument which signalises muscular contraction, but does not register the results. A cord passes round a pulley and is attached by means of a crotchet to one end of a muscle, the other end of which is fixed by a pair of forceps. The pulley carries a long needle, to the end of which a coloured disc is attached. When the muscle contracts, the pulley turns and the disc is raised.

For the purpose of measuring the *duration* of the muscular contraction, it is necessary to have registered: (1) the tracing of the muscular contraction by the aid of the myograph; (2) the instant at which the stimulation of the muscle (or nerve) takes place; (3) the time, noted with the aid of a diapason chronograph. Helmholtz has employed for this purpose the method of Pouillet, in which the duration of an electric current is measured by the deviation of a magnetic needle. In the instrument adopted by Helmholtz, and perfected by Du Bois-Reymond, the current is closed at the moment of stimulation, and opened by the muscle itself at the moment of contraction. There is also an arrangement for loading the muscle with known weights by which the energy of the contraction can be estimated.

The muscular spasm.—When a stimulus is applied to a muscular fibre, or to a bundle of fibres, the excited part is seen to swell and shorten, almost instantaneously; and an appreciable swelling forms on the active part of the muscle. Both these phenomena can be registered, as we have already seen, by the aid of myographs, and we have in this way a graphic representation of the curve of a muscular contraction.

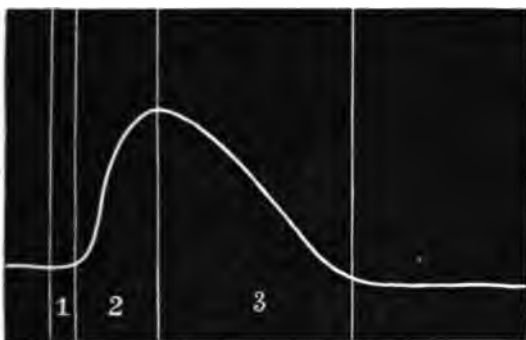


Fig. 40.

Analysis of the curve of muscular contraction.

(1) *Curve of the Muscular Contraction*.—If this curve be analysed, we find that its duration is made up of three unequal periods ;

(a) A primary period (1) during which no change is observable in the muscle, although the stimulus has been applied ; this is known as the *latent period* (*temps perdu*), which is necessary to set the fibres in motion ; this period is about $\frac{1}{1000}$ th of a second.

(b) A second period (2), that of *ascent* of the curve (*period of increasing energy*) which corresponds to the shortening of the muscle : this ascent is at first more rapid, then slower ; the duration is about $\frac{1}{1000}$ th of a second ;

(c) A third period (3), that of *descent* (*period of decreasing energy*), in which the muscle returns to its original length ; this is somewhat longer than the second, although physiologists are not quite agreed on this point.

The *amplitude* of the curve in a tracing is measured by the ordinates ; it is the distance which separates each point from the line of the abscissæ. So long as the original length of the muscle is unchanged, the tracing coincides with this line ; as the muscle shortens, the tracing is gradually raised above it. The longer the muscle fibre, the greater the amplitude of the curve. As a general rule it increases with the strength of the stimulus ; but this increase only goes on to a certain point, and having reached the maximum, the amplitude remains constant (Fick). It is increased by moderate heat, and diminished by

cold, fatigue, or interruption of the circulation ; it diminishes also when a weight is attached.

The *duration* of the muscular shock is reckoned on the line of the abscissæ. As the velocity of rotation of the registering cylinder varies, the tracing occupies but a short extent if the movement be slow, and a great extent if it be very rapid. In order to ensure the accuracy of the calculation, the vibrations of a diapason chronograph which marks fractions of a second are noted on the cylinder. Examined in this way, the period of the muscular contraction is found to vary with circumstances. (a) The latent period shortens when the stimulus is more powerful ; it increases when a weight is attached to the muscle. (b) The causes (already mentioned) which diminish the amplitude, increase the duration of the contraction. The duration is increased when the muscle is loaded ; it is also increased when the muscle is prevented from shortening (Marey). The period of ascent is, generally speaking, shorter than that of descent.

The *form* of the muscular contraction is determined by these two conditions : the amplitude and the duration. It ordinarily presents the following characters : the line of ascent is at first abrupt and nearly vertical ; then, as it approaches the apex it becomes slower and more curved, and is there continuous, by a summit more or less rounded, with the line of descent. The latter is longer and more sloping than the line of ascent, and becomes much more oblique near the lower end. The curve of the muscular energy at each moment of contraction, obtained by the method of Helmholtz, closely resembles the one already described. The return of the muscle to its original length is then gradual, and it remains active during the whole period. Sometimes it does not quite regain its normal length ; a little shortening remains (*contraction remainder*). This may occur when the stimulus has been very powerful ; it is sometimes seen when a small weight has been attached.

(2) *Curve of muscular swelling*.—The form of this tracing is almost identical with that of the muscular contraction ; it merely differs in having a little less amplitude, and, perhaps, a little less precision.

Muscular Tetanus.

If a muscle be subjected to a number of successive stimula-

tions, different results will be obtained, according to the rapidity with which they succeed one another.

(1) If a second stimulus be applied after the termination of the first, a contraction results, similar in all respects to the other; and this may be repeated till the muscle is fatigued.

(2) If the second stimulus be applied during the latent period of the first, the curve will be the same as that of a single one.

(3) The stimulus may be applied during the second or third period of the muscular contraction, and then the curve corresponds to that of the second stimulus, joined to the first contraction; and, if the shocks be repeated, the contraction goes on

increasing till a maximum (proportional in length to the muscular bundle) is reached. If a series of stimuli be applied to the muscle in these periods, the result is a permanent contraction (*tetanus*). If the curve of a tetanised muscle (Fig. 40) be examined, the succes-

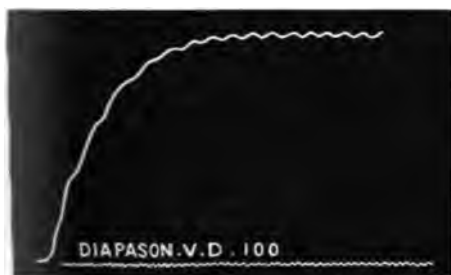


Fig. 41.

sive curves are found to diminish gradually during the ascent, and at last disappear altogether. Fatigue soon ensues, and the muscle then becomes elongated by degrees. A succession of fifteen shocks per second is necessary to produce tetanus in the muscles of a frog, seventy in that of a bird, while three



Fig. 42.

Curves of muscular tetanus obtained at two different velocities (after Beaunis).

per second suffice in case of the turtle (Marey). The longer the shocks continue, the more rapidly is tetanus produced, and everything which causes elongation of the shocks tends to produce this result ; in this way tetanus appears more rapidly in a fatigued muscle. If the stimulus be sufficiently intense, the maximum shortening is immediately reached, and the tracing (Fig. 40) does not present the usual super-position of shocks. The fusion of shocks is due to muscular elasticity, which, as Marey aptly observes, plays, in this case, a part similar to that of the arterial elasticity which converts the intermittent blood-current into a continuous stream.

Transmission of the Wave of Contraction.

The rapidity of the course of the wave of muscular contraction has been measured by three different methods, according as attention has been directed to the swelling of the muscles, the latent period, or the negative phase which precedes it. (a) The method adopted by Aeby, and simplified by Marey, consists in placing the muscle beneath, and in contact with, two parallel levers ; the movements of which are inscribed on a registering apparatus. If the whole of the muscle contracts simultaneously, as after stimulation of its nerve, the levers inscribe similar and parallel curves ; but, if one end be first stimulated, the movements of the distant lever will be found to be a little later than those of the other. The interval is measured by means of the diapason chronograph, and, of course, enables the observer to calculate the rate of progress of the wave of contraction. A modification of this apparatus is used by V. Bezold and Engelmann. (b) Bernstein measures the periods which elapse between the application of a stimulus at two points (placed at different distances from the lever of the myograph), and the resulting contractions. The difference of time forms a datum, from which the required calculation can be easily made. Hermann prefers to apply the method of Pouillet, already used by Helmholtz, for the purpose of measuring the duration of a muscular contraction. (c) At the moment of stimulation each point of the muscle behaves negatively with regard to the points which are in a state of repose. This is called the *negative phase*, and the rapidity of its propagation may be measured like that of the waves of contraction.

If a muscular fibre be examined microscopically at the time of contraction, the swelling produced by the stimulus is found to pass like a wave from one end to the other—*wave of contraction* or *muscular wave* (Aeby); it is distinct only when the muscle is fixed by both ends. Measured by some of the apparatus already alluded to, the velocity has been differently estimated. According to Aeby, Marey, &c., the velocity is about 1 metre per second; according to Bernstein, it is as much as 2 or 3 metres, or more; Hermann, in the case of a living man, has calculated it at 10-13 metres. It is greater in warm-blooded animals than in cold, and is very slow in the cardiac muscle.

The wave of contraction is limited to the fibre stimulated, and not transmitted to the neighboring ones.

The rapidity is diminished by lesions of the muscle (section, &c.); by fatigue, cold, death, action of certain poisons, &c.; also by passage of constant currents.

Physiological muscular contraction.—Voluntary, or reflex, muscular contraction may be registered in the same way as the experimental contractions already alluded to; and the curves are very similar. Like the contraction artificially provoked, it is made of a series of muscular shocks, which unite to form the total shock that acts on the whole muscle. The discontinuity of the voluntary contraction has recently been questioned by Harless, Rouget, and some other physiologists; the chief arguments against it being, that voluntary contraction does not produce secondary tetanus, and never produces more than a simple spasm of the galvanoscopic frog's limb. But it has been shown by Murat and Toussaint that, in artificial tetanus, by increasing the number of stimulations, the duration of secondary tetanus diminishes, and at last it produces but a single spasm in the galvanoscopic limb, as in the voluntary contraction.

Anatomical Phenomena displayed by Contracting Muscle.

When the ends of a contracting muscle are free, it gathers itself into a roundish mass; soft, and semi-fluctuating to the touch, and occupying scarcely a third of the original length. In the living body, however, where the ends are fixed, and the contraction opposed by antagonistic muscles, the shortening never reaches this degree, and hardly exceeds a third of the original

length. The extent of the shortening then for a given muscle depends on the length of its constituent fibres. It is increased by powerful stimulation, and diminishes when the muscle becomes fatigued.

Diminution of Volume.—The increase of thickness does not quite make up for the contraction, and a slight decrease of bulk is observed. It is demonstrated by placing a frog's (or other) muscle in a vessel of water, which has a capillary tube placed vertically above, into which the water also passes. During contraction the water in the tube is seen to sink (Erman). This was at first denied by Gerber; but the results of Erman are now confirmed by most authorities. The diminution of volume has been attributed by J. Müller and Schiff to compression of the air contained in the vessels. Valentin (in the muscles of the marmot during hibernation) has seen the volume to fall from 2706 cc.—2704, and the specific gravity to rise from 1061—1062.

Microscopic changes.—The anatomical changes in contracting muscle can be easily observed with the aid of the microscope. The muscular fibres of insects are most favorable for this mode of examination. When the muscle is fixed at both ends, a wave of undulation passes along the fibres; when one end is free, it is a kind of vermicular movement. It was believed by the older microscopists that the shortening was produced by a zig-zag arrangement of the muscular fibres; and Prevost and Dumas constructed on this foundation a theory of muscular contraction. It is now known that a muscular fibre shortens like a thread of india-rubber; the zig-zag appearance was simply due to contact with the glass slide, which prevented the easy return of the muscle fibres to their original length, and the relaxed fibres present this peculiar form for a little time after the removal of the stimulus.

Of late years, several theories of muscular contraction have been offered. According to Bowman, the individual sarcous elements, whose long axis, in the state of repose, corresponds to that of the muscle, become shorter and wider, so that the transverse measurement is the greater. According to Merkel, in a muscle fibre the two terminal discs (3.3, fig. 36) enclose with the sarcolemma a muscular tube or space which is divided into two by the median disc (1). During repose, the two discs of contractile substance (2.2) are in contact with the median

disc; during contraction they abandon the median disc and approach the terminal discs; but to assume the contracted form it is necessary that the contents should pass through an *intermediate stage of solution*, in which the contractile substance and the liquid portion become intimately mingled. This theory, and especially the solution stage, has been attacked by Ranvier, Engelmann, and others.

According to Schäfer, the phenomenon of contraction is essentially due to the shortening of the muscle rods, which he has described and figured in the water-beetle. They become shorter, while, at the same time, the knobbed ends of adjacent rows are pressed together, so as nearly to touch and form a continuous line. In extreme contraction he considers that they form a definite dark line, while the approximation of the opposite ends, caused by the shortening of the rods, throws the light across the intermediate spaces. In this way the light and dark bands are found to have changed places.

The most elaborate and minute researches have been made on this subject by Engelmann. According to him, both the contractile (anisotropic) and the isotropic parts of the muscle substance present variations of bulk, form, and optic properties during contraction, and these are different for the two parts: both diminish in depth, but the isotropic substance more rapidly and to a greater extent than the other; the volume of the latter increases at the expense of the former—the isotropic substance yields water to the anisotropic, the latter swells and the former contracts; but the two substances do not change places, as can be demonstrated by observation with polarized light. The isotropic substance becomes more refractive, and the anisotropic less so; so that the two parts tend to become equal in this respect, but polarised light always distinguishes them. In the early stage of the contraction the transverse striations gradually diminish, and at last disappear completely. To this stage Engelmann has given the name of the *homogeneous stage*; then, as the contraction progresses, the striations reappear (*stage of inversion*); but, by examination with polarized light, the transverse bands can be made out even in the homogeneous stage.

From what has been said, we must conclude that much research is still necessary before any degree of certainty is arrived at; but one point, at least, seems to be determined; it is, that the anisotropic substance alone is contractile and active, and

that the isotropic segment takes only a passive part in the shortening of a muscle.

Chemical Phenomena of Muscular Contraction.

The chemical phenomena of respiration and metamorphosis, which are always going on during the life of muscular tissue, are greatly increased during the moments of contraction. These changes are studied indirectly by examination of the respiration and urine, &c., and more directly by comparative analyses of muscle tissue at rest, and during contraction; by examination of the venous blood of muscles under both conditions; and by estimating the quantity of oxygen and of carbonic acid absorbed and eliminated.

(1) The comparative chemical analyses have given the following results :—

Acidity. Muscular tissue, neutral when at rest, becomes acid during contraction, and the acidity increases when a heavy load is added to the muscle (Heidenhain). When the circulation is maintained the acidity is not so well marked, the acids being neutralized by the alkalies of the blood (Du Bois-Reymond). The acidity is chiefly due to lactic (or sarcolactic) acid.

Nitrogenous compounds. A diminution of albuminoids in contracting muscle has been observed (Ranke, Danilewsky); but the subject requires further research, as the sources of error are very numerous. With regard to *creatin*, opinions are at variance. Sarakow has observed an increase of creatinin during tetanus, and believes that creatin is converted into creatinin during the contraction of muscle. But later and more extended researches have shown that it is only creatin that is normally present in muscle (Nawrocki, Voit, Basler), with the exception, perhaps, of the heart. It has been sought to decide the question by extirpation of the kidneys, or deligation of the ureters. If the creatin is formed in the muscles, a greater proportion ought to be present after these operations, and this has been reported by Perls, Oppler, and Zalesky; Nawrocki and Voit have not, however, observed such difference, and, even if it exist, it might be referred to the retention in the muscles of the creatin not eliminated by the kidneys.

The existence of *urea* in muscle is also doubtful. The recent results of Picard make its presence normal; but this con-

clusion is still doubted by many high authorities. The results of ligation of the ureters, and of extirpation of the kidneys, have been unsatisfactory; as different observers have reported the most contradictory conclusions. Diminution of urea in the muscles has been reported by Picard after paralysis of the great sciatic nerve. A remarkable fact, observed by Voit, is that in cholera the muscles contain more urea than the blood.

With regard to *uric acid*, experiments made on birds show that after ligation of the ureters this substance accumulates in the muscles, and, similarly, in reptiles after extirpation of the kidneys.

In muscles during tetanisation there is an increase of the *alcoholic extract* (Helmholtz, Ranke) and a diminution of the *aqueous extract* (Ranke).

The total *nitrogen* of muscle has been found, by Danilewsky, to be increased during tetanus; while Ranke has detected no difference in this respect between muscle at rest and muscle in action.

Non-nitrogenous constituents.—*Lactic acid* is one of the principal non-nitrogenous products of muscular action, and it is to it chiefly that the increase of the acidity is due. According to Janowski, the quantity of lactic acid in tetanised muscle is ten times that present in muscle during repose. The variety of lactic acid appears to be the *ethylenic*. *Carbonic acid* is also formed during muscular contraction, of which we shall say more subsequently. The existence of *glycogen* has, of late years, received special attention. Muscles in repose have been found to contain a larger proportion than during tetanus (Nasse, Weiss); and the glycogen of a muscle has been found increased by the section of its nerve, and diminished by its stimulation (Chandelon). According to Weiss, the glycogen of muscle, unlike that of the liver, is fairly constant, and is, to a certain point, independent of alimentation; this view has, however, been contradicted by Luchsinger. Nasse believes that glycogen forms an integral part of the contractile substance; but whether this be the case or not, there seems to be no doubt of its being destroyed at the moment of contraction. Then the question arises, if it is changed into sugar, as many believe, or at once yields more advanced products of metamorphosis, such as lactic and carbonic acids; or again, if the active muscle consumes in its contraction, not only the glycogen,

but also the glucose ; and whether the latter comes from the liver, or is merely derived from the glycogen of the muscle. The *fat* of muscle diminishes during contraction (Ranke, Danilewsky), and it is certain that prolonged immobility tends to promote the accumulation of fat in muscular tissue. According to Sczelkow, the quantity of volatile fatty acids is diminished in muscle during tetanus.

The presence of *reducing substances* in contracting muscle has been demonstrated by Gschleiden and Danilewsky (shown by transformation of nitrates into nitrites and reduction of indigo). The proportion of *water* and *salts* is increased, and especially the phosphate of potash (Danilewsky).

(2). The *respiration* of muscle is more active during contraction; even after a muscle is detached from the rest of the body, and the blood-vessels emptied of blood, there is an increase in the absorption of oxygen and elimination of carbonic acid (Matteucci and Valentin); but the absorption of oxygen is not in proportion to the elimination of the other gas. According to Hermann and Danilewsky, the two phenomena are nearly independent. Even when placed in pure hydrogen or nitrogen, a detached muscle will contract and eliminate carbonic acid, although it contains no gaseous oxygen, or but the merest traces. According to Hermann, indeed, the absorption of oxygen by a detached muscle is merely a phenomenon of putrefaction; and the increase during contraction is only due to the fact, that the movement of the muscle brings its surface into contact with new layers of atmospheric air. It must, then, be admitted, that some substance exists in muscle capable of furnishing carbonic acid, and which is decomposed at the moment of contraction (Stintzing).

The examination of the venous blood of contracting muscle gives similar results. The amount of carbonic acid is increased, and the proportion of carbonic acid formed to the oxygen absorbed, is also greater than during rest.

(3). With regard to the influence of muscular contraction on general nutrition, important information is derived from attending to the renal secretion and respiration. Examination of the quantity of urea passed, however, has given contradictory results; but most recent researches tend to show that there is no direct relation between muscular movement and the amount of urea eliminated. According to Noyes and

Engelmann, the urea is increased only when muscular exertion is carried to extreme fatigue. The same appears to be true of the other nitrogenous constituents of urine, uric acid, and creatinin. A like uncertainty exists about the sulphates and phosphates of the urine; although, according to most authorities, the quantity of the latter is augmented. All observers agree that the chloride of sodium is decreased. The acidity of the urine is notably increased.

Examination of the respiratory excretion has shown that the quantity of oxygen absorbed, and carbonic acid eliminated by the lungs and skin, is increased during muscular action; and the proportional increase of carbonic acid is specially noticeable.

To sum up, then, it may be said that the following chemical phenomena occur during a muscular contraction:—The muscle becomes acid; lactic acid and carbonic acid are formed, and possibly creatin, sugar, and phosphates. It is also probable, although it has not been definitely proved, that a number of other compounds, both nitrogenous and non-nitrogenous, are formed—xanthin, hypoxanthin, inosic acid, uric acid (?), inosite, volatile fatty acids, &c., but in very small quantities, and under conditions still undetermined. Contracting muscle also consumes oxygen, hydrocarbons, especially glycogen, possibly fat (?), sugar (?), and probably a certain proportion of albuminoids.

As to the nature of the substances which are consumed by contracting muscle, three different hypotheses have been advocated:—

(a). *That a muscle in action consumes nitrogenous substances.*
—This theory was specially advocated by Liebig, and since by Playfair, Hammond, &c. The nitrogenous substances consumed by the muscle come either directly from its own substance, or from the nitrogenous principles of the food. On this ground Liebig based his division of foods into *plastic*, which served for the building up of the tissues and for muscular work, and *respiratory* (fats and hydrocarbons), which were used up in maintaining the heat of the body. On this account the two classes of food have been distinguished as *dynamogenic* and *thermogenic*. The chemical facts and analyses already mentioned prevent us from admitting this theory.

(b). *That a muscle in action consumes non-nitrogenous sub-*

stances.—According to this theory, which has been promulgated by Traube, and is admitted now by many physiologists, a muscle may be compared to a machine which produces work by the combustion of carbon and non-nitrogenous substances, such as glycogen, sugar, fats, &c. The chief facts invoked in favor of this theory have been already noticed: the great increase of carbonic acid, which cannot be accounted for by the amount of albuminoids consumed, the fact that the nitrogenous excreta are not proportionately increased, &c., while the amount of carbon consumed, and of carbonic acid produced, approaches very nearly those which, on theoretical grounds, are necessary to produce the work done by contracting muscle. The experiments of Fick and Wislicenus, in the ascent of the Faulhorn, although open to many objections, prove beyond doubt that the great part, at least, of muscular work is produced at the expense of non-nitrogenous substances. Still this theory cannot be exclusively maintained; there undoubtedly occurs, during the contraction of muscle, a disassimilation of albuminoids, which is proved by the marked increase of urea eliminated by the kidneys when muscular action is pushed to fatigue (Noyes, Engelmann).

(c) *That a muscle in action consumes both nitrogenous and non-nitrogenous substances*.—Fick compares the living organism to a machine which produces labor by consumption of carbon, while the framework itself of the machine undergoes a small amount of wear and tear; in case of muscular work the consumption of non-nitrogenous material represents the work done, while the wear and tear of the muscle substance itself is represented by the increase of nitrogenous metamorphosis. On the other hand, Donders, Haughton, and some others will have it, that a contracting muscle consumes in preference the non-nitrogenous substances furnished by the blood, but if these are deficient, it utilises the nitrogenous compounds either of the blood or of the muscle itself; accordingly, in cases of muscular exertion carried to fatigue, some of the nitrogenous combustible material has been consumed, and the urea of the renal secretion is then increased. Whatever modification of this theory be the true one, there can be no doubt that it is the one most in accordance with observed facts.

What the nature is of the chemical processes which take place in contracting muscle, is another question which requires atten-

tion. It was formerly believed that all the changes were due to a process of oxidation, and that the production of carbonic acid was really a combustion of carbon, and similarly with the other products of metamorphosis. But the fact that the carbonic acid produced is not proportional to the oxygen consumed has spoiled this hypothesis, and the fermentation theory is now brought forward to account for this, as for most of the other metamorphoses which go on in the body. A lactic-acid-forming ferment has been supposed to exist, but has not been demonstrated. By their latest researches, Pflüger and Stintzing have been led to the conclusion that the production of carbonic acid during the contraction of a muscle is a simple process of disassociation, as it can be produced at temperatures at which all fermentation is impossible.

Hermann has advanced an ingenious hypothesis for the explanation of the chemical phenomena of contracting muscle. Muscular tissue contains a nitrogenous substance, *inogen*, which is decomposed at the moment of contraction into myosin, carbonic acid, and lactic acid; the two latter substances are carried off by the venous blood, and the myosin undergoes a temporary coagulation, to which the physical change of contracted muscle is due. The arterial blood then conveys to the muscle oxygen and a non-nitrogenous substance which combine with the myosin to form inogen.

Circulation in Muscle.—Ludwig has shown that the blood-vessels of muscle are dilated during its contraction, and the quantity of blood is increased even to double the quantity present during repose (Ranke). Claude Bernard has observed that the vessels of contracting muscle are compressed, and the blood is retained in the capillaries.

MECHANICAL WORK OF MUSCLE.

The extent of shortening varies with the length of the fibres, but the amount of the weight raised is not influenced in the same way. In experiments on the mechanical power of an isolated muscle, it is usually suspended vertically, and the amount of contraction determines the *height of elevation* (*Wurfhöhe*).

In an isolated muscle, leaving out of the question the influence of any attached weight, the amount of shortening depends upon three conditions: (a) it increases with the *strength*

of the stimulus; (b) it diminishes with *fatigue*; (c) it increases with *temperature* to about 130°C (155.4°F .), and diminishes when it reaches 32°C . (89.6°F .) When a weight is attached to the muscle, the conditions of contraction become more complex, and two new conditions are imposed which act in contrary directions: (1) the muscle shortens when stimulated; (2) it undergoes a *primary elongation* from the influence of the attached weight, and there being an increase of extensibility, as Weber has shown, during contraction, there is at each moment a slight increase of length (*consecutive elongation*), and both these factors diminish the total shortening. When a loaded muscle is tetanised, the weight attached is at first raised to a certain *height of elevation* (*Wurfhöhe*), but it immediately descends a little, and remains during the period of tetanus at a medium point, *height of sustentation* (*Hubhöhe*). As a general rule, both kinds of elevation diminish as the load is increased, till a point is reached when the muscle is overloaded, and is unable to shorten.

The amount of useful work performed by a muscle, is represented by multiplying the weight by the height of elevation $W = P H$. When there is no weight attached, the useful work is = 0. When a weight has been raised by a muscular contraction, it falls after the contraction has ceased; the work is converted into heat, and is consequently lost.

To prevent this waste of power it is necessary to support the weight at the point to which it has been raised, in order that the following contraction may raise it still higher. Mechanical contrivances are adopted for this purpose in different kinds of machinery, and Fick has devised on the same principle an apparatus for physiological experiment, which he calls the *arbeitssamler* (*work-collector*).

When a muscle is maintained at the height of sustentation, it performs no external work; still it remains active, and, at the end of a certain time, this activity gives way to fatigue. This form of activity is spoken of as the *internal work* of a muscle or *static contraction*, as distinguished from the *dynamic contraction*, which manifests itself by outer results. This static contraction can only be maintained for a limited time; the arms cannot be kept extended longer than about nineteen minutes (Gaillard).

Although there is an intimate relation between the intensity

of the stimulus and the resulting labor, there is not a definite proportion between the two, and Preyer has failed to establish the *myo-physical* law which he looked upon as the analogue of the *psycho-physical* law of Fechner. As the intensity of the stimulus increases, the resulting work increases also, at first rapidly, afterwards more slowly. The weaker the stimulus, the less difference between the height of elevation of heavy and light weights ; and a minimum stimulus gives the same elevation for all weights.

Absolute force of Muscle.—In experimenting on the amount of work performed by contracting muscle, we find in charging it with heavier weights, that a point is at last attained in which the elongation of elasticity and the shortening of contraction suffice to balance one another, and the weight is not raised when the muscle is stimulated. This weight is the measure of what Weber has called the *absolute force* or *static force* of a muscle, and he has calculated it at 692 grammes for a transverse section of a square centimetre. It can be calculated in case of the human body in the following way :—The body is loaded till it cannot be raised by voluntary effort on the points of the toes ; the static force of the muscle of the calf is equal to

$$\frac{(\text{Weight to be raised}) \times \text{arm of lever of resistance}}{\text{arm of lever of the power}}$$

or—

$$\frac{(\text{Weight of body} + \text{added weight}) \times \text{distance of head of first metatarsal bone from axis of rotation of ankle joint}}{\text{distance of head of first metatarsal bone from insertion of tendo Achillis}}$$

When a muscle has already contracted to a certain point, a smaller weight is sufficient to hinder further shortening than at any previous point of its contraction (Schwann). According to Schwann, the force of muscle diminishes as contraction proceeds, but the contrary result has been obtained by Hermann.

Rapidity of the contraction.—The rate of the contraction varies very much in different muscles, and still more in case of different animals. In man the forearm may be flexed 200 to 250 times per minute, while in certain insects the strokes of the wing may be as many as 330 per second (Marey).

Production of heat in contracting muscle.—The activity of a muscle is accompanied by the production of mechanical work,

or by evolution of heat (internal work). The development of heat which is continually taking place, even during repose, is greatly increased during contraction, and the increase can be made out by observations made on the general temperature of the organism, as well as by that of the individual muscles.

Reaumur long ago observed that the temperature of a bee-hive rises when the movements of the bees become more active, and the same was shown to occur in case of isolated insects by Newport and Dutrochet. The same results were obtained in man by later observers (Hochgeladen, Davy, v. Bärensprung, &c.). An increase of $1^{\circ}.2$ C. was observed by Jürgensen after half an hour's active labor.

Local experiments have been made by Becquerel and Breschet, who inserted thermo-electric needles in the biceps muscle of a living man, and found the temperature to have risen from $.5$ to 1° C. at the end of five minutes after a muscular contraction. Experiments on muscles detached from the body have been made by Helmholtz and others, for the purpose of eliminating the influence of the circulation; and the result has been similar, showing that the elevation of temperature is due to the muscular movement alone. It is produced not only during tetanus but during a single spasm (Heidenhain). This disengagement of heat is preceded by a period of latency (Nawalichin), and was said by some authorities (Solger, Meyerstein, Thiry), to be preceded by a lowering of temperature (*negative variation of heat*), but this has been disproved by Valentin.

The elevation of temperature varies with the *tension* of the muscle (Heidenhain); it also increases with the *degree* of shortening. The increase of temperature progresses more rapidly than the elevation of the weight of the loaded muscle; this is probably due to the diminution of elasticity which takes place during contraction. The elevation of the weight requires an increase of the contracting force, which is accompanied by increased chemical activity, and by increased production of heat. Fatigue diminishes the production of heat.

Relation of heat produced to the mechanical work performed.—It has been supposed that, in contracting muscle the mechanical work produced is but a transformation of the heat disengaged by the chemical changes, and a series of interesting experiments has been undertaken by Beclard with the view of ascertaining the truth of the hypothesis. The result of his

experiments has been that in *static contraction* (when the attachments of the muscle are immovably fixed), there is a greater production of heat, while in *dynamic contraction* (when the ends of the muscle are moveable, and the attached weight is raised), a part of the heat disappears which corresponds to the mechanical effect produced. Fick, in his researches, was unable to calculate a definite equivalence between the heat and the work. According to this authority, the maximum quantity of heat which a gramme of muscle can develop during contraction is 3.1 *microcalories*. (A *microcalorie* is the quantity of heat required to raise a milligramme of water through one degree of the centigrade thermometer).

The specific heat of muscle is .7692, according to Adamkiewicz; .825 according to Rosenthal. Its conductivity for heat is .0431 (Adamkiewicz), or half that of water.

Bruit Musculaire (Muscular susurrus).

When the ear (or a stethoscope) is applied over a contracting muscle, a dull, rumbling sound is heard which has been compared to the distant sound of carriage-wheels (*bruit rotatoire*). This muscular sound is, according to the researches of Helmholtz, one of 19.5 vibrations per second (18—20), and these vibrations are believed to correspond to the successive spasms of which the muscular contraction is made up. This idea is supported by the fact that the bruit of a tetanised muscle may be raised artificially by increasing the number of stimulations, and consequently of the muscular spasms. It was at first said that the muscular sound was one of thirty to forty vibrations, but Helmholtz, in his later researches, has shown that the resonance of the ear itself reinforces the first harmonic of the fundamental sound. He has shown that the muscular bruit is increased by tension of the membrana tympani (in Valsalva's experiment), and lowered when air is injected into the tympanum.

Grimaldi had called attention to the fact that on introducing a finger into the ear a dull, rumbling sound (*bourdonnement*), is heard, which becomes louder when the forearm is strongly flexed; Wollaston referred this sound to the muscular contraction itself, and attributed to it twenty to thirty vibrations per second. The subject has been investigated with great care by Collongues, who has given to the exploration the name of *dynamoscopy*. An instrument which presents at one end a receptacle for the finger, and at

the other end fits into the external auditory meatus, is called the *dynamoscope*. This instrument conducts the sound from the finger tip, and its use has also demonstrated the existence of the *bourdonnement dynamoscopique* everywhere over the cutaneous surface. Its intensity, rhythm, and other characters vary with sex, age, health, and various other conditions. Its cause is not clearly understood. It is certainly increased during the contraction of a muscle, but that it is due to the muscular action only is disproved by the fact that it is continuous. The idea that it is due to the capillary circulation is also disproved by the fact that it persists (for about fifteen minutes) in amputated limbs, and in the finger when tightly constricted by a cord. Another explanation, that it is due to the tonic contraction of the muscles, is more in accordance with known facts: the number of vibrations correspond to those of the *bruit musculaire*; it is diminished during sleep and during anæsthesia; it is increased by electrification, and in cases of cerebral hæmorrhage is completely absent on the paralysed side. On the other hand, we have opposed to this idea its disappearance in the dying, while it persists in certain regions, especially the epigastrium, where it may be heard fifteen or sixteen hours after death. Its longer continuation at the epigastrium has been suggested as a valuable means of distinguishing apparent from real death.

A *bruit de pétilllement* has also been described, which is less regular than the *bruit dynamoscopique*, while its nature is still more obscure.

MUSCULAR ELECTRICITY.

For the purpose of studying the electric currents of muscle various forms of apparatus have been used. One of the most important is that of Du Bois-Reymond, represented in fig. 43. Two glass vessels, V, V, contain a solution of sulphate of zinc.

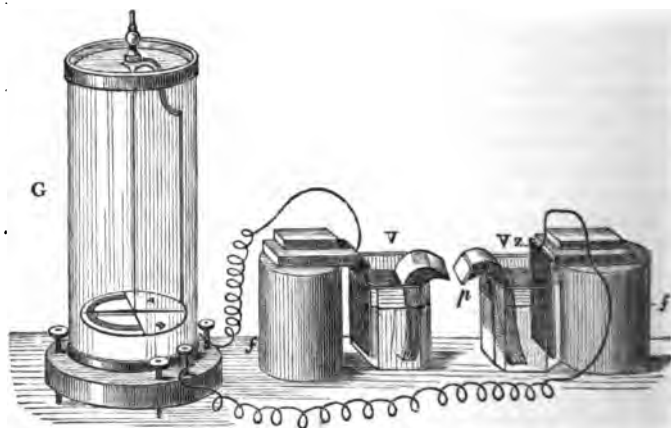


Fig. 43.

Du Bois-Reymond's Apparatus for demonstrating nervous and muscular currents.

A zinc plate, Z, is placed on the isolating support, *f*, and connected with the pole of a galvanometer, G. At the adjacent parts of the vessels are the pads of filter paper, *p*, and on these is placed the muscle or nerve to be experimented on. The current traverses the muscle (or nerve), and produces a deflection of the needle, which indicates the direction of the current. The electrometer of Lippmann has been employed by Marey to show the variations of the electric currents in the fibres of the cardiac muscle during the contractions of this organ, and the telephone of Bell has been used by Hermann to demonstrate the current in muscle during repose. This instrument is interposed in the circuit, and an interrupting wheel placed in the distal chamber, when a sound is produced which corresponds to the number of interruptions.

Physiological rheoscope; patte galvanoscopique.—This name has been applied to the detached leg of a frog, with the greatest possible length of sciatic nerve attached, or the gastrocnemius muscle only (with sciatic nerve attached), may be used. The preparation of the nerve requires special care. It is cleaned from below upwards, and, if properly done, there should be no contraction of the muscle all the time. If the nerve of this preparation be brought into contact with a segment of separated muscle, so as to touch simultaneously the longitudinal and transverse surfaces, a contraction instantly follows.

If a piece of muscle be placed on the paper cushions of Du Bois-Reymond's apparatus, so that the transverse section corresponds to one and the longitudinal surface to the other, the deflection of the needle of the galvanometer indicates the existence of a current in the muscle, which passes from the transverse to the longitudinal surface. The surface of the muscle itself is positive, and that of its transversely divided segment negative. Instead of the transverse section of a muscle its tendon may be taken, which is also negative, and has been called the *natural transverse surface*. The cut surface of a longitudinal section of muscle presents positive electrification. By placing segments of muscle one upon another, like the columns of a galvanic pile, Matteucci has formed true muscular piles. They may also be prepared by placing the nerve of each muscle segment in contact with the transversely cut surface of the neighboring one. If the nerve were placed in

contact with the longitudinal surface, only a very feeble current passes through.

The laws of the electric currents of muscle, which were originally investigated by Matteucci (1849), have been fully determined by Du Bois-Reymond. They are illustrated in the accompanying figure.

(1). There is a well-marked deviation of the needle when the conductor unites the longitudinal to the transverse surface, and the maximum deflection occurs when the middle of the longitudinal surface is connected with the middle of the transverse.

(2). There is a slight deflection of the needle when two points are connected on a longitudinal or transverse surface, which are unequally distant from the middle; or two points unequally distant on the opposed surfaces. In case of the longitudinal surfaces the current passes along the conductor from the point nearer the centre to the one farther off; the reverse is the case for the transverse.

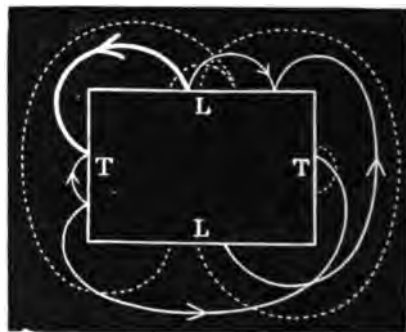


Fig. 44.

Diagram of direction and force of muscular currents. L, longitudinal surface; T, transverse surface.

(3). There is no deviation when two points are connected on the same or on opposed surfaces equally distant from the centre (*symmetrical points*), or when the centres of two opposite surfaces are joined.

In many instances the tendinous part of a muscle is negative, instead of being positive, as the rule is; this has been called by Du Bois-Reymond the *parelectronomio* part of the muscle

In this case it is necessary to make an artificial section, for the purpose of demonstrating the ordinary electric phenomena of muscle.

Hermann's hypothesis.—According to Hermann, whose results have been for the most part verified by Engelmann, the muscle-currents demonstrated by Du Bois-Reymond are the result of the preparation, and do not exist in the normal intact fibres when in a state of repose. The currents observed are due to the destructive action of the air, of cold, or of chemical substances employed. In favor of this idea he brings the fact of the para-electronic condition sometimes seen in muscle, as pointed out by Du Bois-Reymond himself; and the failure of the latter observer to find any evidence of a natural nerve current in his experiments on the living body.

Electric phenomena of contracting muscle.—When a piece of muscle is connected with the galvanometer in the way already indicated, and tetanus is produced by stimulation of its nerve, the needle will be seen to retrace its movement of deflection. This reversal of the natural current is known as *negative variation*. It has been shown by Du Bois-Reymond to be due to a weakening of the natural nerve-current, and not to the production of a new one contrary to the current of repose. This negative variation may act as the stimulus to the nerve of another muscle: if the nerve of the physiological rheoscope be placed on the nerve of a contracting muscle, in such a manner that the first touches both the cut surface and another point on the second nerve, each contraction of the muscle is followed by a contraction of the galvanoscopic frog's limb (*secondary contraction*). Also if tetanus of the muscle be produced by continued stimulation, tetanus of the galvanoscopic limb results (*induced or secondary tetanus of Matteucci*).

We have mentioned Hermann's denial of a natural nerve current, and his chief arguments against its existence. To the current which corresponds to the *negative variation* of Du Bois-Reymond, he gives the name of the *current of activity*. It has been shown by Helmholtz and Bernstein that the negative variation has no latent period; that it commences the instant the stimulus reaches the longitudinal surface of the muscle, and that each point of the stimulated muscle is negative with regard to the parts still in repose. This condition of negativity lasts about .004 sec., and is propagated along the muscle with

the same velocity as the wave of contraction which it precedes, disappearing even before the arrival of the latter.

According to Hermann, when a muscle is stimulated there occurs: (1) an *initial phase*, in which the current within the muscle is directed from the centre towards the extremities (*atterminal current*); then a second phase, in which the (feeblor) current is directed from the extremities towards the centre (*abterminal current*). According to this authority, the phenomena of the currents of activity are explained by the following facts:— (1) transmission (*successive*, not simultaneous) of the stimulus to all points of the muscle; (2) diminution of intensity of the wave of stimulation in its course; (3) negativity of the stimulated points with regard to the points where the excitation has not arrived. Of the current of activity he admits three varieties:—

(1). *Currents of compensation*, which are produced in an injured muscle presenting currents of repose; they correspond to the negative variation;

(2). *Currents of phase* (presenting atterminal and abterminal phases), due to the negativity of a stimulated point with regard to the other points of the muscle;

(3). *Decremental currents*, due to the difference of intensity of the waves of stimulation at two points of application of the conductors of the galvanic current.

Muscular Fatigue.

When the activity of a muscle has been maintained for a certain period, whether by continuous or intermittent contraction, the sensation of fatigue ensues in which the muscle contracts with less energy and with diminished velocity, and soon ceases to contract at all, even by the strongest effort of the will. Under this condition the muscles are affected by voluntary tremblings, and are the seat of a dull pain, which is greatly increased by pressure. Many of the physical properties of muscular tissue are much altered during fatigue.

The *cohesion* is diminished. If both thighs of a frog be broken, the muscles of one stimulated to fatigue, and weights then attached to each limb till the muscles give way, the rupture will be found to take place more easily in the fatigued limb (Liegeois).

The influence of fatigue on the *elasticity* has been disputed ; most believe that this property is diminished. Kronecker has found no alteration, and Volkmann has found first an increase, which was followed by diminution.

The *irritability* of muscle is markedly diminished ; to produce the same degree of shortening, or the same amount of work, a much stronger stimulus is required. The latent period is longer ; the muscular shocks present less amplitude and longer duration (except in extreme fatigue, where the duration is lengthened) ; the fusion of the shocks takes place more rapidly, and the line of descent (which is most influenced by fatigue) indicates a slower return of the muscle to its original length.

A loaded muscle does not become fatigued if allowed to remain inactive.

It has been sought to discover the cause of the phenomena of fatigue, and some have tried to explain it by the exhausting effect of certain products of decomposition, which are formed during contraction. Certain of these substances, especially lactic acid, the acid phosphate of soda, and in a less degree carbonic acid, have the effect, when injected into the blood-vessels of a muscle, of producing the usual phenomena of fatigue. The latter are removed and contractility re-established by injection of carbonate or chloride of sodium. The permanganate of potash (in sol. of .05 per cent.) acts still more rapidly, and its effects would seem to be due, not to any neutralising action, but merely to the supply of oxygen. It is probable, then, that the circulating blood acts on the muscular irritability, both by saturating and removing the acids formed during muscular contraction, and also by conveying to the muscle a constant supply of oxygen.

Rigor Mortis.

The phenomena of rigor mortis (*cadaveric rigidity*) are manifested in muscle a short time after death. The muscles present a hardness and resistance which are easily felt through the skin ; elasticity is lost, the muscles powerfully resist extension, but, once extended, do not return to their original length ; tonicity has disappeared, and, after transverse section, the cut surfaces still remain in contact. It has been asserted by some that cohesion is diminished, and that the muscles are, on that

account, more easily torn ; but this has been denied by many observers, who attribute the diminished cohesion to commencing putrefaction.

The period of its onset is very variable, usually about six or eight hours after death ; the feebler the muscles, the earlier it appears and the shorter its duration ; in this way it occurs very soon in the mature foetus, while it is altogether absent in the foetus of seven months (Mande). Its duration varies from a few hours (or, in exceptional cases, a much less time) up to several days, and usually lasts longer in proportion to the tardiness of its onset.

The rigor mortis commences in the muscles of the lower jaw and neck, then engages the abdominal muscles, those of the upper extremities, trunk, and lower extremities in succession. The heart is also affected by cadaveric rigidity, which causes the so-called *concentric hypertrophy* of this organ. It disappears in the same order in which it came on.

The shortening of the muscles during rigor mortis fixes the limbs in definite positions : the jaws are tightly clenched, the arms close to the side, the fore-arms flexed, the hand clenched, the thumb covered by the other fingers, the lower limbs are approximated, and rigidly extended. The change of position of the limbs takes place with great force, and the force exercised by the cadaveric contraction is greater than that of electric contraction (Walker). A peculiar form of cadaveric rigidity has been observed in case of soldiers killed late in battle, in which the body retains the position in which it was reached by the fatal projectile. It was described long since by Armand, and named by Du Bois-Reymond *cataleptic rigidity*. Its nature has not been explained.

The phenomena of cadaveric rigidity agree pretty closely with those of living muscle during contraction. In an isolated muscle, the rigidity is accompanied by shortening, and also by slight diminution of volume (Schmulewitsch, E. Walker). Its elasticity diminishes, and lactic and carbonic acids are formed. Heat is set free as the muscle passes into the rigid state, and, according to Hermann, the electric currents are found to be similar to those of stimulated muscle. The irritability of the muscle is lost.

The order in which these phenomena are developed is the following :—

- (1) Loss of contractility and disappearance of the muscle current ;
- (2) Modification of elasticity, consistence, and cohesion ;
- (3) Acidity ;
- (4) Loss of transparency, and solidification.

The onset, duration, and intensity of rigor mortis are influenced by many circumstances. It appears earlier in cases of death from exhausting diseases, from hæmorrhage, from convulsive diseases, and in cases of extreme muscular exhaustion, as seen in animals hunted to death. According to Brown-Sequard the more pronounced the muscular irritability at the time of death, the slower the onset, and the longer the duration of the rigor mortis. Heat accelerates and cold retards its appearance, and a temperature of 45°C . (113°F .) causes the immediate onset of rigidity (*rigor caloris*). Artificial rigidity can be produced by obstruction of the arterial circulation, by heat (immersion of a limb in hot water), or by injection into the arteries of distilled water, dilute acids, lime water, potash, saltpetre, carbonate of potash, chloroform, ether, alcohol, &c.

When the rigidity has not proceeded too far, it can be made to disappear by injection of blood into the arteries, by stretching and friction of the rigid muscles, &c.

Since the publication of Kühne's investigations into the properties of *myosin* it is generally admitted that rigor mortis is produced by coagulation of this substance ; and Michelson believes that he has isolated a ferment from muscle identical with the fibrin-ferment of Schmidt, the presence of which would produce its coagulation.

Theories of Muscular Contraction.

The exact nature of a muscular contraction still remains unexplained, notwithstanding the numbers of investigations that have been made on the subject. The hypotheses which have been advanced may be classed under five heads—theories of elasticity, thermo-dynamic theories, electric theories, microscopic theories, and chemical theories.

(1). *Theory of elasticity*.—This has been advocated by E. Weber, Küss, Volkmann, &c. According to Küss a muscle has two natural forms—No. 1 and No. 2—the former being

that of repose, the latter of contraction; but it is not more active in the latter. The stimulus merely changes the elastic form of the muscle, as heat changes the form of a bar of metal. The intimate cause of the change of elasticity is supposed by Volkmann to be some chemical change which modifies the equilibrium of the molecules.

Another form of this theory, advanced by Rouget, has been already referred to. The elongated form of the spiral, of which he believes the muscle fibre to be formed, corresponds to the state of active nutrition, the contracted form corresponds to a suspension of nutritive change, and is then merely a result of physical elasticity.

(2). *Thermo-dynamic theory*.—R. Mayer and Beclard look upon muscle as a machine which, during repose, produces heat only, but during activity, while the amount of heat evolved is increased, a part is changed into movement. This view is, accordingly, closely allied to the chemical theories. Voit, however, believes that it is muscular electricity which is changed into heat and movement, and denies the possibility of the production of the latter from heat.

(3). *Electric theory*.—This theory had been advocated by Prevost and Dumas, and the researches of Du Bois-Reymond seemed to lend support to it. The motorial end plate of a nerve fibre has been compared by Krause and Kühne to the electric organ of a torpedo. The discharge, like a muscular contraction, is made up of a succession of shocks, which unite to form the total discharge; each electric flow has a latent period, like the muscular, of about $\frac{1}{100}$ of a second, and the duration of a partial discharge corresponds to that of a muscular spasm. The muscle, and the electric apparatus of a torpedo, behave in the same way under the influence of temperature, fatigue, strychnine, &c. There are, however, important differences between motor nerves and electric nerves, as in the influence of curara, which does not paralyse the latter, &c.

(4). *Microscopic theory*.—Some authorities (Brücke, Engelmann, Schäfer) believe that the phenomena of contraction are due to certain changes in excessively minute structures, of which the contractile substance is made up. Brücke has named these particles *disdiaclasts*. They should be somewhat similar to doubly-refracting crystals, and a change in their reciprocal arrangement accompanies the process of contraction. Engel-

mann supposes the existence of minute bodies (*inotagmen*), of which the change of form caused the contraction. The *muscle-rods* of Schafer have been already described.

(5.) *Chemical theory*.—This has been already noticed.

It may be observed, in closing, that none of these theories will be found sufficient to explain all the phenomena of muscular contraction, although some seem to throw light on particular phases.

Non-striated Muscle Tissue.

This tissue is made up of elongated fusiform cells, first described by Kölliker, and generally known by his name. They are cemented at their edges by a small quantity of an albuminous, semi-fluid substance, and present a well-developed oval nucleus, containing a nucleolus. According to Rouget, each is made up of minute fibrils, which, instead of being coiled up in form of a spiral, as in the case of striated muscle-fibre, are simply undulating, like those of wool or curled hair. The existence of sarcolemma, although admitted by some, is very doubtful.

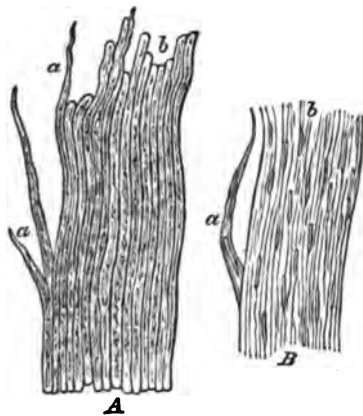


Fig. 45.
Non-striated Muscular Tissue.

The fibre cells are generally arranged in parallel bundles, and these fasciculi, which sometimes interlace in various directions, unite to form larger masses, surrounded by connective tissue sheaths (*endomysium* and *perimysium* respectively). They are supplied by a delicate capillary plexus, less rich than that of striated muscle. The nervous supply is from the sympathetic system, and the termination of the fibres is still the subject of controversy.

The nerve fibres are very numerous in some parts, while they

appear to be absent in certain places ; for instance, in a great part of the length of the ureter.

Smooth muscle tissue is found in the organs specially concerned in the vegetative functions of life : the digestive, circulatory, respiratory, and genito-urinary organs, &c.

A great part of the physiology of smooth muscular tissue is identical with that of the striated. The physical properties of the latter have not been sufficiently studied, but do not seem to present any peculiarities. The chemical properties do not appear to differ from those of striated muscle.

The irritability of smooth muscle is somewhat less in degree than that of the other, but does not appear to differ in kind. There seems to be some difference in the influence of stimuli. In the situations where peristaltic contractions prevail a continued current, when applied in the direction of the wave of contraction, stops it ; the latter is strengthened when the current is applied in the opposite direction. Changes of temperature (heat and cold) act more powerfully on smooth than on striated muscle : hence the names of *thermosystaltic* and *athermosystaltic* muscle, which have been applied to the two forms respectively. Light, which does not influence striated muscle, determines the contraction of smooth fibres, at least in case of those of the iris, as has been demonstrated by Brown-Sequard and H. Müller on the irides of fishes and amphibia, even after extirpation of the eye-ball and removal of the retina.

The irritability of this variety of muscle persists longer after death than that of striated muscle. The order of disappearance, according to Nysten, is as follows : left ventricle of heart, intestines and stomach, the urinary bladder, right ventricle, œsophagus, iris ; then follow the voluntary muscles of trunk, lower and upper extremities ; last in order come the right and left auricles of the heart. When one eye has been left open and the other closed, the pupil of the open eye has been found smaller at the end of thirty hours (Harless).

Certain substances, such as ergotin, quinine, carbonic acid, &c., seem to have a special stimulating influence on unstriated muscle ; but doubt has been thrown on this point by some, and further investigation is required on the subject.

The latent period of stimulation is longer than in striated muscle, and, according to Legros and Onimus, is preceded by an instantaneous relaxation. The advance of contraction is

more gradual, but, once established, it lasts longer. The myographic tracings show a line of descent slower than that of ascent. The contraction is first localized at the seat of stimulation, and is then slowly propagated along the muscular fibre. It does not limit itself to the fibre stimulated; so that, to produce a general contraction, it is not necessary to irritate the nerve as in striated muscle. The wave of contraction passes into the adjacent fibres, and in this way it passes along smooth muscle, unprovided with nerves such as the ureter (Engelmann).

Contraction of smooth muscle-fibre does not (according to Marey) consist of a series of spasms, but of a single spasm, of which the duration may be longer or shorter. They do not seem to be affected by tetanus; yet, Legros and Onimus admit its existence, only allowing that it arrives progressively and without shocks.

Rhythmic contraction of this tissue is seen in some situations, as in the ducts of some excreting glands, in the coats of the arterioles, &c. In case of the cardiac muscle, the contraction resembles, in some points, that of striated fibre.

The occurrence of *rigor mortis* in non-striated muscle has been demonstrated by filling with water a piece of intestine, removed from the body of an animal immediately after death, and tying it at one end, while the other communicates with a vertical glass tube, into which the water rises for some distance. If previously marked, the level of the fluid in the glass tube will be found to ascend when cadaveric rigidity comes on, and fall only when the latter disappears.

MOTION.

It will be convenient to study the physiology of movement after having investigated the structure and physical properties of muscular tissue, by which all active movements are produced.

The great bulk of the animal body is made up of yielding tissues, which have comparatively little power of resisting external pressure, and of maintaining a definite form. The rigidity and persistence of form which are necessary to the maintenance of the functions of life are mainly owing to the skeleton. The physiology of bones and the mechanism of their articulations must accordingly be understood, before the phenomena of station and of locomotion can be profitably investigated.

Mechanics of Muscle.

A muscle attached to two articulating bones presents one of two forms: it is either (1) rectilinear, or (2) reflected at an angle. In the first case, the contraction approximates directly its points of attachment, and the resultant of the activity of the muscle is represented by a straight line, the length and direction of which correspond to that of the muscle itself. In the case of most muscles one of the attachments is more firmly fixed than the other, and accordingly, when the muscle contracts, this end moves slightly, if at all, while the other point of attachment moves towards it. If the course of the muscle presents an angular reflection, its action is produced in one of two ways: (1) in one case the points of insertion are fixed and the point of reflection mobile, when contraction must be accompanied by compression of the underlying tissue; or, (2) the point of reflection is fixed, while the attachments are mobile, when each of the insertions will be found to approach the point of reflection in a straight line.

The action of the contracting muscle on a mobile bone will vary according to the angle which it forms with the latter at the point of attachment.

(1) If the angle be acute, $MM'A$ (Fig. 46), the muscle MM' draws the movable point M' towards M , and so exercises a force which can be decomposed into two: (a) $M'a$, parallel to the mobile bone, and pressing the latter against the fixed bone at the articulation, A ; this part is completely lost; (b) the second component, $M'b$, is perpendicular to the movable bone, and is utilised. The more obtuse the angle between the two bones at the articulation, the larger the proportion of force lost.

(2) If the angle be right (II). In this case all the force is utilised, and the mobile point M' is drawn in the direction of the muscle.

(3) If the angle be obtuse (III). In this, as in the first case, there are two components—one, $M'a$, draws the mobile point M in the direction $M'a$, and tends to separate the mobile from the fixed bone in the articulation, A ; it is the inverse of what occurs in the first case, but its effect is always lost for the movement of the bone; the other component, $M'b$, draws the bone in the direction Mb' , and is alone utilised.

With this construction it is quite easy to calculate the inten-

sity of the force utilised at each instant of the contraction, where the force of the muscle is known. By giving to the line MM' the value of the contracting force of the muscle, and constructing the rectangle of forces, as in the adjoining figures,

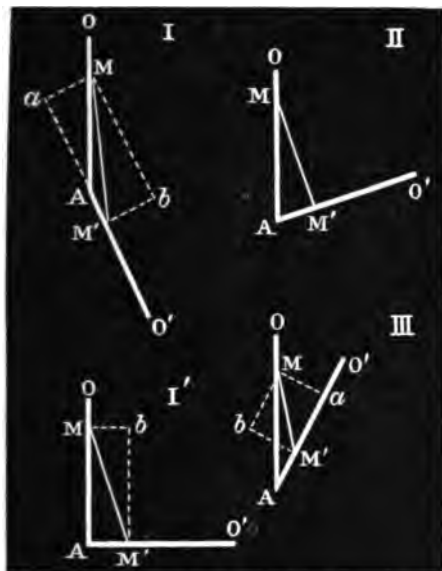


Fig. 46.

we shall have the value of the two factors, Ma and Mb , by comparing their length with that of the diagonal, MM .

All the movements conveyed to a bone by a contracting muscle belong to one of these cases. Many muscles do not pass through the three positions, but cease to act before having attained their momentum (position in which the traction is perpendicular to the movable bone). It is also well to remember that, according as a muscle is at the beginning or end of its contraction, there is a mutual pressure of the articular surfaces, or a tendency to their separation. In the case of muscles which cross several articulations, the calculation of the action on any one of these is more complex; it can be

done approximately by supposing the others fixed, but this is not what occurs in the living body.

In every movement the mobile bone represents a lever, of which the power is at the place of attachment of the contracting muscle, and the resistance at the variable point at which is applied the resultant of the weight, and other obstacles to the displacement of the movable bone. According to the respective positions of these three points, the moving bone represents a lever of the first, second, or third kind.

In the *lever of the first kind*, the fulcrum is placed between the power and the resistance. The support of the head in the erect position is an instance. The power is behind, at the attachment of the occipital muscles, the resistance at the centre of gravity of the head, and the fulcrum at the occipito-atlantoid articulation, which is between those points. The extension of the trunk on the pelvis, of the thigh on the leg, of the leg on the foot, are other examples of this form of lever, which, for obvious reasons, is called the *lever of station*.

In the *second kind of lever* the resistance is placed between the power and the fulcrum. The arm of power is always longer than the arm of resistance, and, as the force brought to bear is inversely proportional to that of the arms, while the velocity is in the same proportion, this lever is specially advantageous in the exercise of physical energy. Hence it is called the *lever of force*.

Examples of the second kind of lever are not common in the human body; rising on tip-toe is the best example, an action in which great expenditure of force is necessary. The power is at the insertion of the tendo Achillis, and the resistance (formed by the weight of the body), is placed at the tibio-tarsal articulation. Another example is shown in the act of opening the mouth. (Fig. 47).

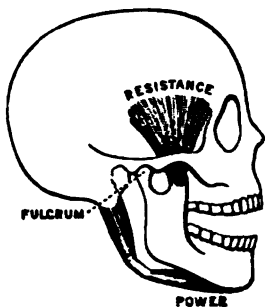


Fig. 47.

In the *third kind of lever*, the proportional length of the arms is reversed, and the power is placed between the fulcrum and the resistance. The result is, that rapidity of movement is

gained at the expense of force, and it is on this account called the *lever of velocity*.

The third kind of lever is that most frequently employed in man's movements. A good example is that of flexion of the fore-arm; the fulcrum is at the articulation of the elbow, the power at the insertion of the flexors (biceps and brachialis anticus), and the resistance at the middle of the fore-arm (Fig. 48).

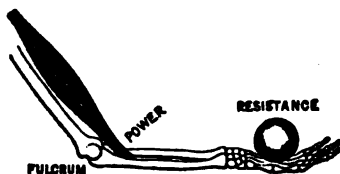


Fig. 48.

In order that a muscle should displace by its contraction a given bone, it is necessary that the other bony attachment should be fixed; this must be done by the action of other muscles attached to it, and so on till we pass, step by step, to the central parts of the skeleton. The fixation of this jointed system of levers is best seen when we prepare for some movement requiring great muscular force; the muscles are then all contracted, and the body becomes rigid and inflexible at all parts, so as to form a solid support to the muscles which have to execute the appointed movement.

The efforts of muscular action always manifest themselves either by *traction* or by *pushing*, and, in either case, can be estimated by the instrument called the *dynamometer*, which is formed by an oval elastic spring, of which the two sides can be approximated by pressure in the direction of the short axis, or traction in its long diameter. The degree of approximation is indicated by the deviation of a needle on a graduated scale, the divisions of which correspond to known weights.

Station.

This term is used to denote the position of equilibrium in which the body can be maintained for some time, without displacement. The position may be one of standing, sitting, or lying, but the essential condition in all is, that the perpendicular from the centre of gravity falls within the base of support.

Centre of gravity.—The situation of the centre of gravity has been differently estimated by different observers: E. Weber placed it at the level of the promontory, Meyer in the canal of the second sacral vertebra, and Harless a little lower down.

According to the last-named observer, if the height of the body be represented by 1000, the distance of the vertex from the centre of gravity should be = 414, and of the latter from the feet = 586. It is a little lower down in the female, and a little higher in the infant.

The centre of gravity of the *trunk* is placed on the line which passes from the xiphoid cartilage to the eighth dorsal vertebra (tenth, according to Horner), and in a transverse plane passing a little behind the heads of the thigh bones.

Base of support.—The base of support in standing is formed by the line joining the feet. It obviously increases with the separation of the feet, and still more in sitting. The maximum is attained in the lying posture.

Maintenance of the line of gravity within the base of support.—If muscular contraction were necessary to maintain the line of gravity within the base of support, fatigue would soon follow, and the attitude could not be maintained. To obviate this necessity, the human body is so formed that, in the upright position which characterises man, the body, down to the ankle-joint, forms a rigid whole along a line of articulations, each of which forms a lever of the first order, and these joints are so constructed that the necessity for muscular action is reduced to a minimum, and the solidity is maintained chiefly by the tension of the ligaments.

The centre of gravity of the head falls a little in front of the axis of rotation of the occipito-atlantoid articulation, and a slight tension of the occipital muscles is necessary to prevent its falling forwards. The required effort is very slight on account of the shortness of the arm of resistance. Very little, if any, muscular action is required to maintain the erect position of the spine in ordinary conditions.

The centre of gravity of the trunk falls a little behind the axis of rotation of the hip-joints, but the body is kept erect by the tension of the ligament of Bertin and of the tensor vaginae muscle. Lateral inclination is prevented by the tension of Bertin's ligament, and, according to Duchenne, by the action of the middle and small gluteal muscles. In the articulation of the knee, the centre of gravity is placed a little behind the axis of rotation, and extension is maintained by the quadriceps, aided by the tensor vaginae femoris, with its ilio-tibial ligament.

Every oscillation of the body, of course, displaces the centre of gravity, and equilibrium has to be instantly re-established by muscular action. The muscular sense then comes to play a very important part in the maintenance of position, as it is through it that we estimate the amount of force necessary to re-establish the equilibrium of the body.

The varying sensations of pressure conveyed to the extremities of the plantar arch by the oscillations of the centre of gravity, play an important part in the maintenance of equilibrium; also vision, by showing the position of the fixed objects around, &c.

In the position of standing evenly on both legs (*station symétrique*), the centre of gravity is placed in the median plane, and considerable muscular action is necessary to maintain it, on which account fatigue soon supervenes. In standing with the weight of the body resting on one leg (*station insymétrique, station hanchée*) much less muscular action is necessary, and fatigue is not felt so soon. On this account the position is instinctively adopted, when we have to stand for any considerable time.

LOCOMOTION.

Many devices have been employed for the purpose of studying the details of the movements which the human body is able to execute by the action of its various muscles on the different parts of the skeleton.

Method of the brothers Weber.—The subject of the experiment walked on a perfectly horizontal plane for a length of forty metres. The length and mean duration of each step was obtained by dividing the length of the course by the number of steps. A special apparatus in the sole of the boot indicated the time of contact with the ground, and by deducting this from the time of a double step, the duration of the period of oscillation was calculated. The inclination of the trunk was measured by means of a telescope, placed 100 metres from the ground paced on, by which a certain marked point on the trunk was observed.

The amplitude of the vertical oscillations of the trunk was measured by observing a certain point of the trunk, by means of a horizontal telescope, furnished with a micrometer.

Marey's method.—Marey has invented several instruments for this purpose. One part of his apparatus is a shoe, with a hollow sole, containing a *tambour à levier* (sometimes two; one corresponding to the heel, and the other to the anterior part of the foot), while the subject of the experiment bears on his head an apparatus which registers the vertical oscillations. This consists of a *tambour* placed on a *planchette* resting on the vertex; the lever of the *tambour* bears a mass of lead, which acts by its inertia;

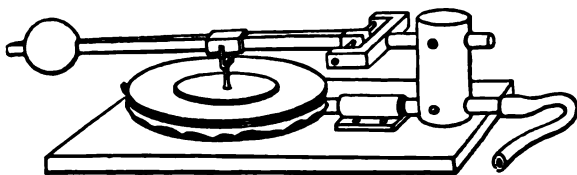


Fig. 49.

Marey's apparatus for exploring the movements of walking and running.

whenever the body is raised vertically, this mass resists, and the pressure which it exercises on the tambour is transmitted to the lever, which is raised; the reverse occurs when the body descends. In addition to these, there is a registering apparatus, which is carried in the hand, and which communicates with each of the tambours.

The whole is illustrated in the annexed wood-cut.



Fig. 50.

In addition to these parts of the registering apparatus, Carlet used registers of the oscillations of the trunk and of the movements of inclination.

Odograph.—This is the name given by Marey to an instrument made to register the movements in walking through a long distance. The registering apparatus consists of a hollow cylinder, which is kept in uniform rotation by clockwork, and covered by a roll of paper graduated in millimetres. The velocity of rotation corresponds to definite lengths on this paper; and parallel to the axis of the cylinder moves from below upwards, a style, which is acted on by a spring placed within a hollow column. By a special contrivance the style, when it has arrived at the top of the cylinder, is made to fall to the bottom again, so that several inscriptions can be made without confounding the tracings.

Vierordt's method.—The subject of the experiment walks on a long strip of paper placed on the ground, and along a line previously traced on it to indicate the direction. The boot on each foot contains three chambers of colored liquid; one for the heel, and two for the anterior part. The colors for right and left differ. Each foot then leaves on the paper, in walking, three colored marks; and these show the length of each step, the separation

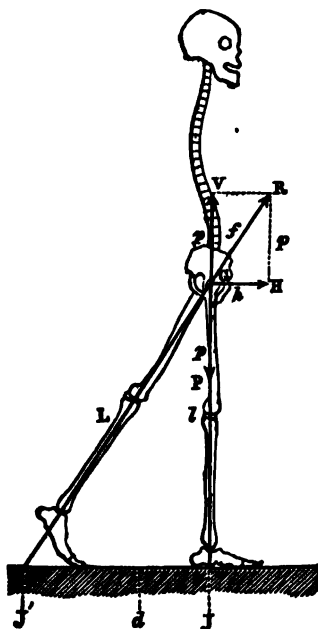


Fig. 51.

between the feet, the position of each foot, and the angle made by each with the line of direction. To show the elevations and depressions of the different parts of the body, strips of paper are placed vertically, and extending along the line of march, and horizontal tubes are attached to the different prominences, calcaneum, trochanter, &c., from which colored fluids are ejected at each step.

Walking is distinguished from running by the body never quitting the ground completely. Either leg bears alternately the weight of the body, and pushes it forward by changing the base of support at each moment.

If the forces which come into play in walking are decomposed, G (Fig. 48) representing the centre of gravity of the body, we see that two forces act on it: one represented by the leg JG, maintains equilibrium, the other produced by the extension of the leg J'G, pushes the centre of gravity in the direction GR, and is able to be decomposed into two elements, one vertical, GV, which tends to elevate the centre of gravity (to it the vertical oscillation produced in walking is due); the other, GH, is horizontal, and determines progression. The two legs are seen to form a right-angled triangle, of which the hypotenuse is formed by the posterior extended limb, and the perpendicular (larger side) by the supporting limb, while the shorter side J'J represents the length of a step. The latter is called by Marey a *demi-pas*. According to his idea, a step (*pas*) is the "series of movements which are executed between two similar positions of the same foot."

Movement of the foot in walking.—In ordinary walking the heel is first placed on the ground, and by continuing its movement, the whole sole is soon applied; the heel is then raised and the anterior part of the foot alone is in contact with the ground, and at last the contact is brought to an end by lifting off the point of the foot. The period of contact of the sole of the foot with the ground is called by Marey the *temps d'appui*.

The Step.—The double step of Marey has been already defined. The ordinary step is the time of double support (when both feet are in contact with the ground), plus the time of oscillation of one leg. In examining the step we must consider both its length and its duration.

(1.) *Length.*—It has been found that as the length of the step increases, there is a proportional increase of pressure on the anterior points of support of the foot, while the pressure on

the heel remains unchanged. This is due to the fact that the body is lowered more at the moment when the point of the foot touches the ground, and requires a greater pressure on the anterior part of the foot to elevate it.

(2.) *Duration*.—The duration of the steps decreases, as the brothers Weber have shown, in proportion as the length increases. It is the duration which determines the rapidity of walking; and, according to the Webers, in extremely rapid walking the time of double support is reduced to zero. This has, however, been contradicted by Carlet, who found that, even in the most rapid walking, both feet are on the ground together for an appreciable time during each step.

At the commencement of the step one of the legs is situated beneath the centre of gravity of the body, and the other, the oscillating limb, is placed farther back. At the moment when the foot is placed on the ground, the supporting limb (*jambe portante*) is extended, or but very slightly flexed. According to Carlet, the limb is a very little flexed at this moment, but it becomes rapidly extended, and extension is complete when the heel is quitting the ground. An elongation of the limb is thus produced, which raises the trunk and carries it forward. When the extension of the limb is complete, the foot is raised from the ground by flexion of the knee, while the foot and toes remain extended, and the leg passes into the movement of oscillation (*jambe oscillante*).

The oscillating limb, once raised from the ground, swings from behind forwards, while it is at the same time carried forwards by the movement of the trunk. According to the brothers Weber, the limb oscillates in pendulum fashion, and after purely physical laws; but the more elaborate researches of Duchenne, Marey, and Carlet have demonstrated the intervention of muscular action (for example, the psoas, iliacus, and tensor vaginæ femoris for flexion of thigh, &c.). But in addition to this, physical forces undoubtedly play an essential part, including atmospheric pressure, which maintains the mutual contact of the coxo-femoral articular surfaces, nearly to equilibrate the weight of the leg.

During walking, the great trochanter is found to oscillate both in the vertical and horizontal directions. Horizontally, the great trochanter is carried to one side, when the corresponding foot rests on the ground, and to the opposite side

when this limb oscillates; at the middle of the period of unilateral support, the two trochanters are found in the same vertical plane; at every other moment the trochanter of the posterior limb is placed behind that of the anterior. Vertically, the minimum elevations of the trochanters is found during the time of double support. Either trochanter is raised during the time of oscillation of the corresponding leg, and attains its maximum elevation; it is lowered when the foot is placed on the ground, raised a little at the middle of the period of unilateral support, and regains its maximum elevation at the moment when both feet are on the ground.

Movements of the Trunk.—Four kinds of movements of the trunk are observable during walking :—(1) oscillation; (2) inclination; (3) rotation; (4) torsion.

Oscillation.—Besides the advance of the body in walking, the trunk executes both lateral and vertical oscillations, which have been studied by Carlet (taking the symphysis pubis as the point of exploration). *Horizontally*, the symphysis leans most to one side, at the moment when the foot of that side is in the midst of its time of support, and the amplitude of its oscillations increases with the length of the step. *Vertically*, the pubis is found at its maximum elevation when one of the legs is in the midst of its time of support, and the other in the midst of its period of oscillation; the minimum elevation is in the middle of the period of bilateral support. The amplitude of the vertical oscillations is about thirty-seven millimetres.

Inclination.—The body, in walking, leans to the side of the limb which supports it, and attains its maximum at the same moment as the maximum vertical oscillation of the same side. At the same time the trunk inclines forwards, making, with the vertical plane, an angle usually not above ten degrees, but increasing with the length of the step.

Rotation.—When the arms are fixed to the sides of the trunk, one side of the pelvis and the corresponding shoulder are found to rotate with the horizontal movements of the great trochanter. This form of movement corresponds to the amble of quadrupeds.

Torsion.—When the arms are free, the side of the pelvis and corresponding shoulder are found to rotate in the opposite direction to those of the corresponding lower limbs. These movements correspond to the ordinary gait of quadrupeds.

Movements of the upper limbs.—The oscillations of the upper limbs in walking, when the lower are free, are in the opposite direction to those of the lower limbs. They have been shown by Duchenne to be due to muscular action, and not merely to pendulum-like oscillation, as was formerly believed.

RUNNING.

While, in walking, there is always a period during which both feet are on the ground ; in running, there is a time in which both feet are raised from the ground, and the body is momentarily suspended in the air. The leading differences in the mechanism of the two movements are as follows :—the movement of extension of the leg is much more powerful, and by it the body is projected from the ground ; during the time of suspension the lower limbs oscillate, the one which last touched the ground is placed a little behind the other, and continues its movement of oscillation while the latter is on the ground.

During the time of running the body undergoes vertical oscillations, which, according to the brothers Weber, are less than in walking, while Marey has arrived at a contrary result. The vertical oscillations correspond to the times of contact of the feet with the ground, and not with the time of their elevation, as might at first sight be supposed.

CHAPTER IX.

PHYSIOLOGY OF THE NERVOUS SYSTEM.

VIEWING it from the broadest stand-point, the nervous system forms an apparatus which connects the peripheral sensory surfaces (skin, mucous membranes, organs of sense) to the muscles and other deep structures (glands, &c.). If we take the most rudimentary form of nervous system, it is limited to a simple cord (3) uniting a sensitive surface (1) to the contractile structure (2) (Fig. A.). In the fresh water hydra, cells have been found, of which the superficial part is nervous in function, and epithelial in position and structure; while the deep part, which is larger in size, and distinctly contractile, represents the muscular element. As we ascend the developmental scale, the

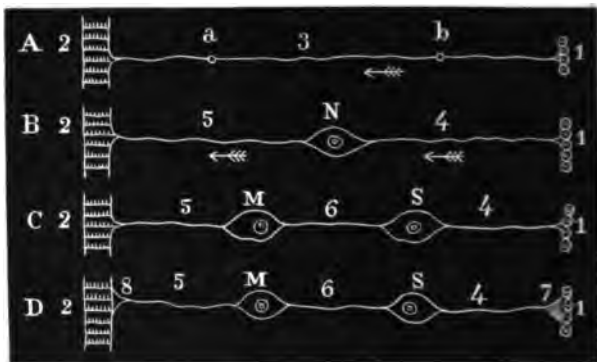


Fig. 52.

next step would be an accumulation of nervous substances at one part of the connecting cord (B. Fig. 52); this would represent the first attempt at the formation of a nervous centre. Of the two segments into which the nervous cord is divided by the centre (N), the one (4) connected with the sensory surface (1) is

called the *sensory* (*afferent*, or *centripetal*) nerve, while the segment (4) connected with the contractile element is called *motor* (*efferent*, or *centrifugal*). The nerve centre appears to be specially concerned in the *production* of nerve-force, while the nervous cord itself acts as a *conductor*. The nerve centre is a reservoir of nerve-force, which is set free on the application of some stimulus to the sensory surface, and is transmitted to the muscles and other organs by the centrifugal nerves.

But a more frequent arrangement is that represented diagrammatically at c, in which two cells are placed on the nervous cord that connects the peripheral with the contractile structure. That connected with the sensory nerve is the *sensory cell* (s); that connected with the centrifugal nerve is the *motor cell* (m). The intermediate portion of the nervous cord (6) is distinguished as the *intercentral, commissural, or intercellular nerve*.

The highest stage of perfection is reached when special *peripheral nerve organs* are developed in connection with the ends of the nerves, sensory or motor (D, 7, 8).

The nervous system is accordingly made up of three essential parts:—

- (1). *Nerve fibres*; these are the conductors of nerve force.
- (2). *Nerve cells (nerve centres)*; organs of production and disengagement of nerve force.
- (3). *Peripheral nerve organs*, sensory and motor.

We shall proceed first to examine the structure of the different kinds of nerve tissue, and afterwards consider their functions.

Nerve Fibres.—Of these there are two kinds: (a) the *medullated* (*white, cylindrical, double-contoured, fibres à myeline*), and (b) the *non-medullated* (*gray, pale, gelatinous fibres of Henle, fibres of Remak*). The diameter of the former varies from $\frac{1}{15000}$ th to $\frac{1}{13000}$ th of an inch; the former are generally from $\frac{1}{80000}$ th to $\frac{1}{60000}$ th of an inch in thickness.

(a) Each medullated nerve-fibre is surrounded by a delicate, slightly elastic membrane, the *sheath of Schwann* (*primitive sheath*). Within this is the *white substance of Schwann* (*medullary sheath, myelin*), which resembles fat in staining black with osmic acid. This sheath is interrupted at regular intervals by annular constrictions (*nodes of Ranvier*), where the white substance wholly disappears (Ranvier), or is only thinner than

elsewhere, as Rouget asserts. On either side of a constriction, the fibre presents a slight enlargement.

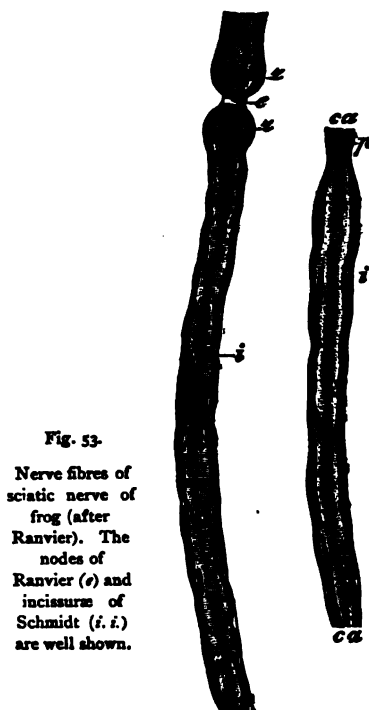


Fig. 53.

Nerve fibres of sciatic nerve of frog (after Ranvier). The nodes of Ranvier (*v*) and incisurae of Schmidt (*i. i.*) are well shown.

Along each interannular segment the medullary sheath presents oblique notches (*incisura*), first noticed by Zawerthal (1864) and afterwards more fully described by Schmidt and Lantermann. These cut off cylindro-conical segments of the medullary sheath, which overlap one another like the tiles of a roof. On the inside of the sheath of Schwann is an oval nucleus, surrounded by a thin layer of protoplasm, corresponding (usually) to about the centre of each of Ranvier's nodes. It is looked upon by this author as the nucleus of the cell, which by elongation and modification comes to

form the interannular segment, and of which the cell-wall is represented by the sheath of Schwann. The lines of junction of the latter with the sheaths of adjoining segments, can be demonstrated by the nitrate of silver staining, which defines the intersegmental cementing substance. Still, although admitted by most histologists, some observers believe Ranvier's constrictions to be merely the result of manipulation, and having no existence during the life of the nerve.

On the inner side of the medullary sheath is a thin layer of protoplasm (*sheath of Mauthner*), which separates it from the outer surface of the axis-cylinder. This layer, according to

Ranvier, becomes blended at the annular constrictions with the layer which is placed on the outer side of the medullary sheath; and the two are connected at the incisuræ of Schmidt by small prolongations. According to this description, the myelin is enclosed in a protoplasmic sheath, which encloses it in the form of limited segments. In some fibres these segments are found merely as uneven scales, forming an irregular covering for the included parts (*sheath of Kuhn*). According to some observers, this sheath is formed of a horny substance (*neuro-keratin*); and when the myelin and axis-cylinder are removed by digesting with trypsin, it forms the scaffolding of the nerve-fibres, in the form of an internal and external sheath, enclosing a system of compartments corresponding to the notches of Schmidt (Kühne, Ewald, Rumpf, &c.). The interval between the medullary sheath and the axis-cylinder is the *peri-axial space* of Klebs. According to Ranvier, the absence of myelin at the interannular constrictions allows the blood-plasma to pass into the axis-cylinder for its nutrition.

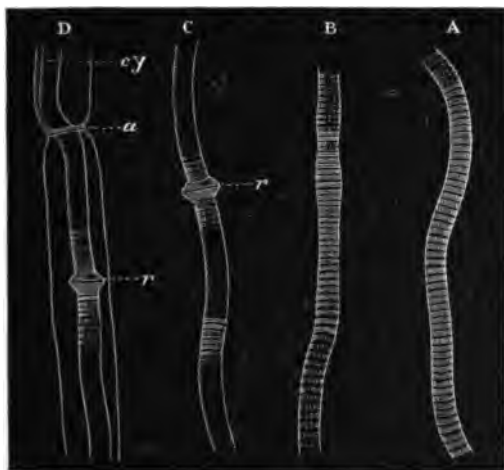


Fig 54.

Nerve-fibres and axis-cylinders of sciatic nerve of rabbit separated and treated with a solution of nitrate of silver (after Ranvier). A, and B. Axis-cylinders showing the striae of Frommann. C. Axis-cylinder showing the biconvex swelling (*r*). D. Nerve-fibre, showing one of Ranvier's nodes at *a*; *r*, biconvex swelling; *cy*, biconvex swelling.

The *axis-cylinder* (of Purkinje and Rosenthal) occupies the central part of the nerve-fibre. It was originally described by Remak under the name of the *primitive band*. It is formed by a bundle of excessively fine fibrils (*primitive fibrillæ* of Max Schultze). This view of its structure, however, although admitted by most, is contradicted by some. According to Fleisch the axis-cylinder is entirely fluid. Roudanowsky asserts that it is formed by an epithelial tube filled with liquid. According to Engelmann the axis-cylinder is interrupted at the annular constrictions; but, according to Ranvier, with whom most other observers agree, it is continuous along the whole length of the nerve-fibre. Near the annular constrictions it presents biconvex enlargements.

The axis-cylinder is easily stained by coloring matters (carmin, &c.). After preparation with nitrate of silver, the cementing substance at the annular constriction is colored, and the silver solution, passing in, stains for a short distance the albuminous substance around the axis-cylinder. This gives rise to the formation of the *latin crosses* (see Fig. 54.) which appear



Fig. 55.

Intercostal nerve of mouse formed by a single funiculus, stained with nitrate of silver. The endothelium of Henle's sheath, and some of Ranvier's nodes are shown.—
X 200 diam. (after Ranvier).

on the sheath after this mode of preparation (Axel Key and Retzius). The stained portion of the axis-cylinder presents transverse striations, first pointed out by Frommann (1864). The *striae of Frommann* are placed by Klein in the layer of albuminous substance (sheath of Mauthner) between the medullary sheath and the axis-cylinder.

(b). The *non-medullated nerve-fibres* (*fibres of Remak*) possess no medullary sheath, and resemble the axis-cylinders of the medullated nerve-fibres. According to Ranvier and Klein, some have no sheath of Schwann, but these, as well as the others, present nerve corpuscles, placed here and there on their outer surface.

These nerve-fibres abound in the sympathetic system, and when the medullated fibres of either the cerebro-spinal or sympathetic systems are traced to their terminations, they are found to lose the medullary sheath and assume the characters of non-medullated fibres.

If a transverse section be made of one of the cerebro-spinal nerves, and the divided surface examined with sufficient care, the following parts can be distinguished (Axel Key and Retzius):—

Epineurium (*tissue connectif perifasciculaire* of Ranvier), the connective-tissue sheath. It is composed of interlacing bundles of connective-tissue fibres, in the meshes of which are found blood-vessels and lymphatics, as in other connective-tissues; also the ordinary fat-cells, connective tissue corpuscles, and Waldeyer's plasma cells.

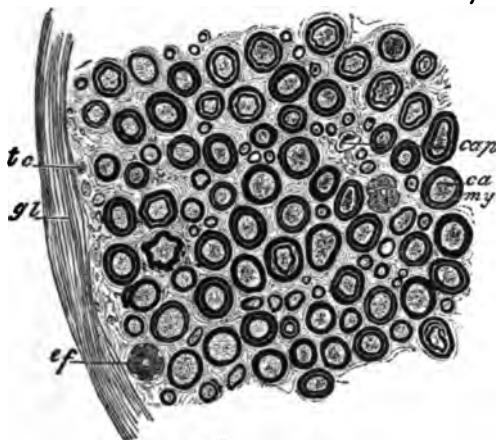


Fig. 56.
Transverse section of great sciatic nerve of dog (after Ranvier). *GL* (gaine lamelleuse) perineurium; *tc*. tissue-connective intrafasciculaire) endoneurium; *ef*. nerve-fibre divided close to one of Ranvier's nodes.

Perineurium (*gaine lamelleuse* of Ranvier).—This is the sheath of lamellated connective-tissue bundles, between which are placed the ordinary flattened corpuscles, while the lamellæ are separated by interlamellary lymph-spaces, and enclose the bundle (*funiculus*) of nerve-fibres within. Within the perineurium is a lymph-space.

Endoneurium (*tissue connectif intrafasciculaire*).—This is a more or less homogeneous membrane, which passes in between the individual nerve-fibres, and is made of a closely fitted mesh-work of fibrous bundles. Within the endoneurium is a lymph-space surrounding each nerve-fibre; and these are connected on the outside with the perineural lymph-space, which surrounds each funiculus.

Around the individual nerve-fibres is a special membranous sheath, lined by a continuous layer of endothelial cells (*Ranvier's sheath of Henle*, Robin's *perineurium*).

The *blood-vessels* ramify in the perifascicular and intrafascicular connective tissue sheaths, and form longitudinal meshes, while the capillaries alone pass beneath Henle's sheath to come into contact with the sheath of Schwann.

The *lymphatics* commence in the perifascicular connective tissue. If an interstitial injection be thrown into this tissue, it fills the lymphatics and passes on to the lymphatic glands; while if the injection be introduced within the perineurium, it passes along the length of the nerve, as in a closed tube, without getting into the lymphatics at all.

Nerve-cells.—These peculiar corpuscles are found in the grey matter of the nerve centres (brain, spinal cord, ganglia); also in the ganglia of the sympathetic system, where they present some peculiarities to be described afterwards.

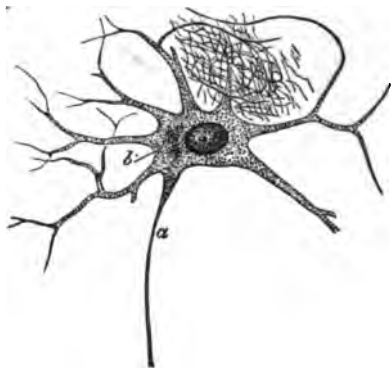


Fig. 57.

Multipolar nerve-cell from grey matter of spinal cord. *a*. Axis-cylinder process (after Gerlach.)

The cells of the cerebro-spinal nerve-centres are of two varieties—the polar and the apolar; the former giving off one or more processes, the latter none. The apolar corpuscles are probably but growing cells. Of the processes, two kinds have been described by Deiters—the *axis-cylinder* and the *protoplasm*. The axis-cylinder process is single (one from each cell) and unbranched, and after proceeding for some distance receives a covering of myelin, then a sheath of Schwann, and becomes in this way continuous with the axis-cylinder of a medullated nerve-fibre. The protoplasm processes, on the other hand, are observed to branch repeatedly, and there are generally several from a single corpuscle, although there may be but one. By the repeated divisions of the processes, a delicate network is formed (Gerlach's *nerve-*

plexus), which seems to be continuous with the primitive fibrils; of which, like the axis-cylinder process, these prolongations seem to be made up. Some believe that these processes anastomose with others from neighboring cells, but the connection is very hard to demonstrate, and is entirely denied by some.

The connective tissue of the nerve centres (*neuroglia* of Virchow, *reticulum* of Kölliker), presents marked peculiarities. It is made up of three distinct elements—a matrix, fibres, and cells. The matrix is quite homogeneous when fresh, but becomes granular when treated with chromates. The fibres are extremely fine, and form a delicate meshwork, like that of adenoid tissue; and the cells (*neuroglia cells of Deiters*) are stellate connective-tissue corpuscles.

Development of Nerve Tissue.—The *nerve-cells* come from the embryonic cells of the medullary groove, which, increasing in size, become granular and send out processes, which then proceed to branch in various directions. According to Robin, these cells are at first nuclei (*myelocytes*), but most deny this. The same authority states that they afterwards multiply by very active segmentation.

The development of nerve-fibres is still involved in great obscurity, and several theories have been advanced on the subject. (a) According to some observers, all nerve-fibres, both central and peripheral, come from the central mass of nerve cells, the growth proceeding from the centre towards the periphery by multiplication of these cells. (b) Another theory, originally advanced by Von Baer, is, that the nerve-fibres are developed locally, by histological differentiation of the adjacent cells. (c) A peculiar view, advocated by Hensen, is, that the central nerve-organ and the peripheral terminal apparatus form a bi-cellular structure, of which the nerve-fibre is the commissure. This idea would coincide very nicely with the rudimentary nervous apparatus sketched in the beginning of this chapter. At an early stage of development the future medullated nerve-fibres closely resemble the fibres of Remak; and according to some, the latter are but the arrested form of development of nerve-fibres.

Robin, as well as Ranvier, believes that nerve-fibres are formed by the fusion of fusiform cells, end to end, and asserts that the first part to appear is the sheath of Schwann, while most observers make the axis-cylinder the primary element, the medullary sheath and the sheath of Schwann being secondary formations. According to the researches of Rouget, Ranvier, and some other observers, the nerve-fibres are outgrowths from the central nerve-cells, and develop by degrees from the centre towards the periphery. Rouget, who has studied the development of nerve-fibres in the tadpole, &c., has found that the first elements to appear in the batrachia are fine fibrils, identical with the terminal fibrils of the sensory nerves of the adult, and with the branching fibrils of the processes of the nerve-cells; these corresponding to the primitive fibrillæ of the future axis-cylinder. These fibrils are ensheathed by a thin layer of protoplasm, forming elevations at intervals, so as to give the film a beaded appearance. Nodules of this

substance gather at intervals and form nuclei. The fibrillæ multiply and form the axis-cylinder; the outer layer of the protoplasmic sheath becomes condensed, and forms a membranous sheath (afterwards the sheath of Schwann), and the fibre at this stage presents the characteristic appearance of a non-medullated nerve-fibre. These fibres grow further, branch, and divide, while the nuclei multiply; the medullary sheath gradually appears around the axis-cylinder, and the sheath of Schwann is formed from the outer membranous layer of the protoplasm already noticed. Although the myelin is in greater quantity round the nuclei, it is nowhere interrupted; and, according to this observer, the whole nerve-tube and its contents (axis-cylinder and its primitive fibrillæ, medullary sheath, protoplasmic sheath, and sheath of Schwann) form an uninterrupted whole from the centre to the periphery.

According to Ranvier, the axis-cylinder is alone continuous and developed from the processes of the central nerve-cells; the sheath of Schwann and the medullary sheath are secondary and local formations.

The essential anatomical facts derived from the preceding description are:—

- (1). The nerve-cells anastomose or are connected with one another by means of their processes, or through the medium of the delicate nerve-plexus of the grey matter;
- (2). The nerve-fibres are continuous with the processes of the central nerve-cells;
- (3). The nerve-cells communicate with the muscular fibres on one hand, and with the epithelial surfaces on the other, by means of nerve-fibres.

I.—PHYSIOLOGY OF THE NERVE-FIBRES, OR OF THE WHITE NERVE-SUBSTANCE.

A.—CHEMICAL PROPERTIES OF THE WHITE SUBSTANCE.

The *reaction* of nervous tissue is neutral, or slightly alkaline, during life, but after death, or when exhausted (by the action of strychnia or of electricity), it is found to be acid (Funke). Acidity also appears when the tissue is heated to 45°—55° C. (113°—131° F.). According to Gschleiden, the grey substance is acid during life, while the white substance is neutral or feebly alkaline.

The following substances are found in nerve tissue:—

- (1). *Albuminoids*: chiefly albuminate of potash, a substance analogous to myosin, and an albumin coagulable at 75° C. (167° F);
- (2). *Lecithin, cerebrin, nuclein*:

(3). *Nitrogenous extractives*: creatin, xanthin, hypoxanthin, uric acid, urea, leucin;

(4). *Non-nitrogenous extractives*: cholesterin, inosit, palmitic acid, lactic acid of fermentation (especially in the grey substance);

(5). *Salts*; the chief being the alkaline phosphates, and chloride of sodium;

(6). *Water*.

This analysis shows a close resemblance to the composition of muscle-tissue; the chief characteristic distinctions being the presence of cerebrin and cholesterin, and the different variety of lactic acid.

According to Kühne and Ewald, the skeleton of the nerve-fibre is formed by a special dense substance (*neurokeratin*), which does not yield to the action of gastric or pancreatic juice, as the medullary sheath and axis-cylinder do. The proportion of solids to water in the substance of white and grey matter is not the same.

The following analyses of brain substance are from Petrowsky:—

Per 100 parts.	Grey substance.	White substance.
Water	68.3508 ..	81.6042
Solids	31.6422 ..	18.3958
Per 100 parts of solids.		
Albuminoids and glutin	55.3733 ..	24.7252
Lecithin	17.2402 ..	9.0045
Cholesterin and fats	18.6845 ..	51.9088
Cerebrin	.5331 ..	9.5472
Substances insoluble in ether	6.7135 ..	3.3421
Salts	1.4552 ..	.5719

The following table gives the results of four analyses of the salts of brain tissue (Geoghegan):—

	In 600 parts.	In 500 parts.	In 500 parts.	In 500 parts.
Cl	.720	.215	.660	.532
PO ₄	.843	.478	1.008	.696
CO ₃	.478	.122	.274	.165
SO	.136	.051	.068	.066
Fe(PO ₄) ₃	.006	.048	.049	.016
Ca	.003	.010	.007	.011
Mg	.001	.034	.030	.036
K	.978	.290	.889	.760
Na	.601	.225	.557	.390
Total	3.775	1.473	3.542	2.672

The following table (from Weisbach) shows the influence of age on the percentage of water existing in nerve tissue :—

	Age.	Brain.		Convolution- tions.	Cere- bellum.	Pores.	Medulla Oblongata
		White Matter.	Grey Matter.				
Men	20—30	69.56	83.36	78.47	78.83	73.46	74.43
	30—50	68.31	83.61	79.59	77.87	72.55	73.25
	50—70	70.19	83.80	79.61	78.89	72.01	72.24
	70—94	72.61	84.78	80.23	80.34	72.74	73.62
Women	20—30	68.29	82.62	79.20	79.49	74.03	74.07
	30—50	70.31	83.06	77.29	78.90	72.20	72.98
	50—70	68.96	83.84	79.69	78.45	71.40	73.06
	70—91	72.20	83.95	80.17	79.79	72.41	73.37

In comparing the composition of grey and white nerve-substance, the grey is found to contain more water, lecithin, albuminoids, and salts, while the white matter has more cholesterin and cerebrin. The spinal cord and nerves contain a large proportion of cholesterin. The brain of the embryo contains more water and less cholesterin than that of the adult, and the proportion of water increases as we descend the animal scale. The brains of the insane are very poor in cholesterin.

The composition of *neuroglia* closely approaches that of connective tissue. According to Kühne and Ewald, however, it is made up of a special substance, *neurokeratin*, which is allied to horny tissue.

Micro-chemical characters of nerve-tissue. The *axis-cylinder* is formed by an albuminoid substance, which gives a red color with Millon's reagent, and is changed to acid-albumin by acetic acid. It swells up in dilute acetic acid (by which it is dissolved); it is also dissolved by water, ammonia, bile, dilute solutions of potash and of sodium chloride; it is hardened by mercuric chloride, chromic acid, and bichromate of potash; it is colored brown by the tincture of iodine, and stains easily with coloring agents (carmin, hæmatoxylin, &c.); nitrate of silver causes the appearance of transverse lines (Frommann's striæ).

The white substance of Schwann is made up of cholesterin, lecithin, cerebrin, albumin, and probably fatty matter. It is dissolved by alcohol, by ether, and by oil of turpentine; it swells up in water; it is reddened by the action of sulphuric acid, while osmic acid stains it of an inky black color.

The *sheath* of Schwann seems to belong to the collagenous

substances ; it is dissolved by alkalis. Digestion in gastric or pancreatic juice dissolves out the axis-cylinder and myeline, leaving the investing structure of *neurokeratin* (Kühne, Ewald).

After death the nerve-substance becomes hardened, and this change has been compared to the rigor mortis of muscle, and theoretically attributed to the coagulation of a substance analogous to myosin. No such substance has, however, been extracted, and the change may be due merely to the consolidation of the fats contained in the myelin (Beaunis).

B.—PHYSICAL PROPERTIES OF THE WHITE SUBSTANCE.

The *consistence* and *cohesion* of the white substances are pretty strong in the nerve cords throughout the body, but very slight in the nerve centres ; the difference being due to the large proportion of dense connective tissue in the structure of the former. A weight of 20—25 kilogs. has been found necessary to produce rupture of the median and ulnar nerves, and 54—58 in case of the sciatic. The rupture is preceded by a very considerable elongation.

The *extensibility* of nerves is at first proportional to the weight supported, but after a certain point is reached, the elongation does not increase in the ratio of the weight, so that the curve of elasticity of nerve tissue is represented by an *hyperbola* (Wundt). The co-efficient of elasticity of nerve fibres is 1.0905 (Wertheim).

The *specific gravity* of white substance is greater than that of grey ; that of the former being 1.041, of the latter 1.034 (Sankey).

The *capacity for imbibition* of white substance tissue is very considerable ; it absorbs 50 per cent. of its weight of water (Marcet). It is greater when the nerve tissue is in a state of activity than during repose, and becomes very great when it has been fatigued by over-exertion or when it is tetanised (Ranvier). The nerves behave in the same way as the spinal cord or brain. If the sciatic nerve of a frog be isolated, and placed in water of the temperature of the animal, the nerve, at the end of twenty minutes, will be found to have lost its physiological properties, from the water having penetrated into the nerve tubes.

C.—PHYSIOLOGICAL PROPERTIES OF NERVES.

Nutrition.—The two great parts of which a nerve-fibre is made up require to be borne in mind in studying its nutrition. The axis-cylinder differs in mode of nutrition, as in its histological structure, from the other part of the interannular segment, formed by the sheath of Schwann and the myelin. According to Ranvier, the plasma, after escaping from the capillaries, passes in through the cementing substance at the annular constrictions, and perhaps at the notches of Schmidt, and so finds its way to the axis-cylinder; it is in these situations that the coloring matter is found to penetrate in nitrate of silver and other preparations. After supplying nutritive matter, the plasma passes into the endoneural and perineural lymph spaces, from which it is taken up by the lymphatics.

The nutrition of the nerve-fibres, as experiments have proved, is under the influence of the central nerve-cells, which form trophic centres. If the fibres be separated from the latter by section of the nerve, they rapidly undergo degeneration. This change first manifests itself in a segmentation of the myelin, which goes on till this substance is broken up into isolated lumps. The axis-cylinder then proceeds to divide into wavy segments, and these gradually break up and disappear completely. At the same time all the protoplasmic structures of the nerve undergo a granulo-fatty degeneration, the nuclei of the interannular segment multiply by division, and at last nothing remains of each nerve-fibre but the sheath of Schwann, enclosing a protoplasmic mass, containing nuclei, and fatty granules, and scattered clumps of ovoid masses of myelin.

In the regeneration of nerves, as in their original formation, the new growth is from the centre. The axis-cylinders of the central end of a divided nerve become enlarged, and present longitudinal striations; they soon divide, so as to form young nerve-tubes, which have at first no medullary sheath. These grow into the cicatrix, and come to join the peripheral segment of the divided nerve, either by passing into or between the old medullary sheaths. According to results of most of the experiments made on mammals, divided nerves seem to regain their activity in a period of 2—5 weeks, but it seems to require a very much longer time in case of man (12—15 months, according to Letievant).

The nervous tissues have been shown, by experiment, to be the seat of *respiratory changes*, similar to those of muscle; the bloodless brain of a pigeon was found to absorb oxygen and eliminate carbonic acid (Ranke).

The products of metamorphosis of nerve tissue are not well known; the albuminoids are chiefly used up (Byasson, Liebreich). Urea would seem to be one of the chief products. According to Flint, cholesterin is one of the principal products of nerve-waste; but his results have not received general favor. Phosphates (derived from lecithin) also seem to be a product of nerve-waste.

Excitability of nerves.—This is the property which a nerve possesses of entering into activity, under the influence of a stimulus. The activity manifests itself in some obvious way, by some modification of motion, or expression of sensation; but, apart from this external manifestation, the activity of a nerve is, in itself, latent. Still, by the aid of our present means of investigation, we can always ascertain whether a nerve is or is not in an active state. The most important index is the *negative variation* which a nerve, as well as a muscle, undergoes during activity.

As the most obvious manifestation of nervous action is the shortening of the muscle to which it is distributed, the latter is chosen as the means of measuring and registering the degree of irritability of nerves. In order to estimate nervous irritability, we must know accurately both the intensity of the stimulus and the result produced.

This property requires for its due manifestation the absolute integrity of the nerve, with due activity of circulation and nutrition. Still, even in normal conditions, it is extremely variable, and is in a constant state of instability. Alternate intervals of activity and repose appear to be most favorable to its maintenance. Prolonged repose diminishes, and may even abolish it altogether, by leading to degeneration of the nerve-fibre; and over-stimulation, on the other hand, destroys it completely. Very slight mechanical stimulation causes an increase of irritability (Harless, Wundt, &c.), but any strong mechanical interference with a nerve injures its integrity, and so diminishes its irritability.

Constant electric currents modify the irritability of nerves, and the resulting phenomena have been studied with great care

by Pflüger, who describes the altered conditions under the name of the electro-tonic state (*electrotonus*).

During the passage of a constant current the excitability of the nerve is diminished on the side of the positive pole or anode (*anelectrotonus*), and increased on the side of the negative pole, or cathode (*catelectrotonus*). The intra-polar segment of the nerve always contains a point (*point indifférent*) in which the excitability is neither increased nor diminished; this point, in case of feeble currents, is in the neighborhood of the anode; in case of strong currents it is placed near the cathode. The influence of electrotonus is greatest in the neighborhood of the poles, and extends for some distance along the extra-polar parts of the nerve. The same variations of irritability follow the application of other stimuli.

The state of *catelectrotonus* is produced immediately on the closure of the current, and rapidly increases at first, afterwards slowly diminishing in intensity and in extent. *Anelectrotonus* is more slow to develop, and, like the other, decreases after having reached its maximum. The variations of irritability travel from the poles along the nerve in the form of a wave, of which the velocity can be measured (Wundt, Grünhagen). If the force of the nerve-current is increased, the change of irritability increases to a maximum, then gradually diminishes to zero, but to reappear again in an inverse sense. After rupture of the polarising current, the irritability returns to its original state, but only after passing through an inverse phase, an increase at the anode (*positive modification* of Pflüger), and diminution at the cathode (*negative modification*). The positive modification disappears very gradually; the negative modification, on the other hand, disappears very quickly, and is immediately replaced by a positive modification (lasting up to fifteen minutes). The total result of the rupture of the current is, accordingly, an increase of irritability.

The influence of electrotonus on sensory nerves has not been sufficiently studied; a diminution of excitability both for *anelectrotonus* and *catelectrotonus* has been found by Zurhelle.

Experiments made on living man, with the view of determining the conditions and results of electrotonus, have not given any satisfactory evidence.

Electrotonic changes of irritability, similar to those of nerves

have been demonstrated in muscle, but they are entirely limited to the intra-polar region.

Heat causes a temporary increase, followed by a diminution of the irritability of nerves; when above 50° C. (112° F.), it causes a diminution of irritability, which is completely abolished at 65° C. (149° F.); when the temperature has not reached this point, it reappears on cooling. *Cold*, when suddenly applied, increases the irritability of nerves; when continued, the irritability diminishes, but in case of an isolated nerve, or after death, it tends to preserve it a longer time. *Imbibition of water*, as already mentioned, causes complete abolition of nervous irritability. *Dessication* at first increases it, but the latter disappears completely when the nerve has lost forty per cent. of its water.

The action of *chemical substances* varies with their nature and degree of concentration. Neutral salts, weak acids, urea, veratria, &c., increase the irritability; it is abolished rapidly by acids, by alkalies, or by salts in concentrated solution, probably by disorganization of the nerve substance. Some volatile substances, such as ether, chloroform, &c., cause first an increase, and afterwards a diminution, of nervous irritability. It seems to be independent of oxygen, for it is retained as long in a moist vacuum (Ewald), or in indifferent gases (Ranke), as in the air. A revivifying effect on the nervous excitability has been attributed by Severini to ozone, but its action is still uncertain.

Chemical and mechanical irritants sometimes cause an increase of irritability, similar to that observed during the passage of the polarising current, as mentioned above; and, in this way, stimulants which would have had no effect when used alone, can produce a visible result (muscular contraction, &c.), when they follow other applications which increase the irritability of the nerves.

The irritability of nerves is not equal in all points of their course. That the irritability of motor nerves increases as we recede from the muscle is a fact pointed out for the first time by Budge, and afterwards more fully investigated by Pflüger. Pflüger experimented at first on nerves separated from the nerve centres, showing that stimulation of the distant parts produced a more powerful contraction than that of the parts near the muscle; and, on Heidenhain raising the objection that

section of a nerve increased its irritability in the neighborhood, Pflüger repeated his experiments on undivided nerves, and met with the same results, basing on these facts his *avalanche theory*, to which we shall subsequently return. Heidenhain found, in experimenting on the sciatic nerve of the frog, that the irritability diminished in receding from the muscle, then increased till the original degree was attained, which it gradually passed, and gained its maximum point at the level of the plexus, from which it diminished in passing towards the spinal cord. Hermann is disposed to believe that in the normal nerve all points are of equal excitability, and with this view Beaunis agrees.

In case of the sensory nerves, Matteucci, and more recently Rutherford, have found that the reflex movements produced by stimulation were more powerful as the stimulant was applied nearer to the nerve centres.

When the nerves are separated from the centres, the irritability is at first greatly increased, partly from the removal of central inhibitory influence, and partly from the increase of irritability produced by section. This increase of irritability soon gives place to a diminution, and finally to a complete disappearance.

Nerve stimuli.—The physiological stimuli to nervous activity during life, pass, in some cases, from the nerve centres, and in others from the peripheral organs (organs of special sense, skin, mucous membranes, &c.). But in experimental physiology we have recourse to artificial stimulation, the same agents for the most part being used, as those applied to muscle, of which we have already given an account. The effect, with stimuli of equal intensity, is greater in case of nerve than in that of muscle.

When the agent applied acts gradually and continuously, no manifestation of increased activity follows; in order that the nerve may be excited, it is necessary that the modification in its condition should be produced with a certain degree of rapidity, and this law applies to all stimuli. We can produce complete destruction of a motor nerve by pressure, cautiously applied and gradually increased, without causing a single muscular contraction.

(1) *Mechanical Stimuli.*—Every mechanical stimulation, rapidly applied (such as pricking, section, stretching, rapid

pressure, &c.), causes an increased activity of the nerve. If the mechanical application be at all violent, the nerve will probably suffer so much that its irritability is destroyed; but if cautiously used, the sensibility to subsequent stimulation may be retained. When a succession of mechanical stimuli are rapidly applied in this way, the nerve may be thrown into a state of continuous activity, manifesting itself, in case of a motor nerve, by tetanus of the muscle to which it is distributed.

Mechanical Tetanisation.—To produce this condition Du Bois-Reymond employs a small-toothed wheel which rotates with sufficient rapidity, and of which the teeth strike the nerve as it revolves. Heidenhain has devised an instrument to which he has given the name of *tetanomotor*, which consists of a small hammer that strikes the nerve, and is itself kept in motion by the revolution of a toothed wheel. The apparatus is so constructed that the nerve is gradually moved, so as to present to the hammer, successively, points nearer to the muscle.

(2) *Physical Stimuli. Electricity.*—This is the stimulus most frequently employed in experiment, and requires the most careful study. The stimulation may be produced by constant currents, by induced currents, or by the discharges of a condenser.

(a) *Constant Currents.*—In using the constant currents the following apparatus is necessary: (1) a battery of which the elements are the most constant possible (Grove's and Daniell's are among the best); (2) a *rheocord* to graduate the intensity of the current; (3) commutators to change the direction; (4) apparatus for the opening and the closing of the current (Du Bois-Reymond's key, mercurial interrupter, &c.); (5) interrupters for the production of intermission; (6) electrodes (especially thenon-polarisable), for placing in contact with the nerve; (7) a myograph or some other registering apparatus.

The breaking tetanus (Ritter's tetanus).—When a nerve has been traversed for some time (half-an-hour or more) by an ascending or descending current of considerable intensity, there often follows, on the breaking of the current, a tetanic contraction, which lasts eight or ten seconds. This tetanus disappears when the current is closed in the same direction, and is strengthened when the current is closed in the opposite direction. If, on the other hand, the current be feeble or applied but for a short time, or, if the irritability has been diminished by the death of the nerve, there follows, instead of the breaking tetanus, but a prolonged contraction, or merely a single spasm. According to Pflüger, this tetanus is due to the powerful stimulation produced by the disappearance of the anelectrotonus: it ceases when the muscle is separated from the anelectrotonic segment, as can be done in case of a

descending current, by section of the nerve at the intrapolar point of indifference.

This tetanus presents many analogies with the closing tetanus already mentioned. According to Engelmann and Grünhagen, both these varieties of tetanus depend on latent stimulation, acting on the whole length of the nerve (desiccation, changes of temperature, &c.); stimuli, which in the normal state, are unable to produce tetanus, will cause it to appear when the irritability of the nerve has been increased in certain points, as at the cathode, at the closing of the current, and at the anode, when the current is broken. This explanation reconciles the facts of tetanus produced by the constant current with the general law of nerve stimulation. The secondary contraction produced by the tetanus of the constant current, is always a single shock, and never a tetanus.

Volta's alternatives.—It was observed by Volta that when a nerve is traversed by a constant current, the irritability of the nerve is diminished or abolished for the closing or opening in the opposite direction; but, if the current remains long closed, the irritability reappears for the current of the same direction, and disappears for one of the opposite direction, and so on. It was shown by Rosenthal and Wundt that this formula was inexact, and they arrange it in the following terms:—A constant current increases the irritability of the nerve for the breaking of a current of the same direction, and for the closing of a current of opposite direction; it diminishes the irritability for the closing of a current having the same direction, and for the rupture of a current having the opposite. These laws, however, hold good only for weak and medium currents; for very strong currents, the breaking tetanus is weakened by the closing of the current, and strengthened by breaking, whatever the direction (Pflüger). The alternatives of Volta have also been explained by himself with the help of his theory of electrotonus.

B. Action of induced currents on nerves.—The induced current of rupture (produced by interruption of the induced current), in the same way as this current itself, is rapidly established, and at a very high tension; the induced current of closing (produced by closing the induction current) is, on the other hand, more slowly established, and at a very feeble tension. For the purpose of studying the effects of these two, special induction apparatuses have been devised to dissociate them, and pass into the nerve either the induced current of breaking, or that of closing. One law governs the stimulation of nerves by induced currents; it is that with an equal intensity of the induced current, the nerves are excited much more powerfully by that of rupture; and this law applies to sensory nerves as well as to motor (Chauveau, Fick). The maximum stimulation is always at the cathode.

The action of induced currents on motor nerves can be easily recorded by means of the myograph registering apparatus, when the interruptions do not succeed too rapidly. Beginning

with a feeble current, we first see the shock of rupture appear, the amplitude of which increases in proportion to the intensity of the current ; when the current attains a certain intensity, the shock produced by closing is seen ; for each interruption then we have two muscular spasms instead of one, a powerful one produced by the breaking, and a feebler produced by the closing of the current ; as the intensity of the current is increased, these at last become equal.

When the frequency of the induced currents is increased to a certain degree, the resulting fusion of the shocks leads to muscular tetanus.

At a certain frequency the induced currents of opening and closing are found to neutralise one another.

Action of static electricity, and of the discharges of the condenser.—The effect of the discharges of the condenser is similar in nearly all respects to that of the currents obtained from instantaneous piles.

Unipolar stimulation (Chauveau).—This mode of stimulation, already referred to, has yielded, in the hands of Chauveau, many interesting results :

(1). In every healthy nerve there is a certain strength of current which gives an equal degree of activity to the two poles (positive and negative). The contractions produced by both positive and negative stimulation are then equal in force and in duration.

(2). Beneath this intensity the effects are unequal, the activity of the negative pole is the greater.

(3). Above this intensity the case is reversed, the positive pole is found to be more active.

(4). In case of sensory nerves, the inequality is manifested in the opposite way to what occurs in case of motor nerves. With equal currents the application of the negative electrode is much more painful than the positive.

(5). With regard to the breaking contractions, when the intensity of the current is gradually increased, the breaking contraction appears sooner with the negative stimulation than with the positive, increases with the intensity of the current, till a maximum is reached, then remains stationary, and at last disappears altogether. The negative contraction appears only after the positive has commenced to decrease, and, in like manner, first increases, and then decreases.

(6). For a feeble current the positive contractions are simple spasms ; when the current is strong, tetanus lasts during the passage of the current. In case of negative stimulation, tetanus is more easily produced.

(7). When the nervous system is intact, a part of the shortening remains after breaking the current. This is best seen after tetanisation with the positive current. After section of the spinal cord this is no longer seen. After the cord has been destroyed for some time, the tetanisation by strong positive currents is exchanged for very short closing shocks.

(8). Simple division of the nerve gives rise to the same results as destruction of the spinal cord, with the difference that the section at first gives a remarkable inversion of the activity of the poles.

(9). Instantaneous discharges act like continued currents, and more easily provoke contraction with the negative than with the positive pole; when the intensity of the current increases, both positive and negative stimulations become equal, and contrary to what is seen in case of continued currents, the equality is maintained as the strength of the current increases.

(10). When the intensity of the induced currents and of static discharges is increased beyond a maximum, which is soon reached, the muscular shocks remain the same.

Effect of heat on the nerves.—The influence of temperature on nerves has been variously reported by different observers. Pickford has asserted that any sudden change of temperature acts as a nerve-stimulant. According to Valentin and Rosenthal, a temperature below -4° C. ($24^{\circ}.8$ F.) or above $+35^{\circ}$ C. (95° F.) applied to the motor nerves of the frog causes a contraction. Eckhard, on the other hand, while admitting the influence of the low temperature named, affirms that an elevation of 66° to 68° is necessary to have any effect. Grüntzner, in a series of elaborate experiments, has arrived at the conclusions, that different degrees of temperature are required to stimulate the different classes of nerves, vaso-motor nerves (except those of the skin) not being affected. The only researches made on man have been by Weber, who, in plunging the elbow into a freezing mixture, so as to chill the ulnar nerve, found that pain, but not contraction, in the part supplied by this nerve was the result.

Chemical stimuli.—The action of chemical agents is, broadly speaking, less than their action on muscle (perhaps on account of the density of the nerve-sheaths). Some act merely by withdrawing the water from the nerve; drying of a nerve alone produces fibrillary contractions, going on to tetanus. Distilled water has no action on nerves. Neutral salts, chloride of sodium (4—30 per cent.), alkalies, acids, glycerine, alcohol, creasote, carbolic acid, urea, bile, solutions of biliary acids, &c., all act as nerve stimuli. The action of these re-agents on sensory nerves is still uncertain.

Transmission of the nerve-current.—This requires the integrity of the stimulated nerve-fibre, and presents the following peculiarities:

(1.) *It is limited to the stimulated nerve-fibres.*—The medul-

lary-sheath has been supposed to act the part of an insulator, but this function has not been demonstrated. A peculiar phenomenon, the so-called *paradoxical contraction*, was at one time supposed to be contradictory of the rule. If the sciatic nerve of a frog be removed with its two branches, and the muscles to which they are distributed, stimulation of one branch is found to cause contraction in the muscles supplied by the other branch as well as its own. But the phenomenon is now known to be merely one of electrotonus, for the paradoxical contraction will not take place if the nerve be stimulated low down near its muscle, or if mechanical or chemical stimulation be employed.

(2.) *It passes in both directions, and presents the same characters in both motor and sensory nerves.* (a) When a nerve is excited, the phenomenon of negative variation is seen in both ends. (b) If a sensory and a motor-nerve be divided, and if the central end of the sensory nerve be united to the peripheral end of the other, cicatrisation easily takes place. If the central end of the sensory nerve be then irritated, evidence of pain in the muscles is at once manifested. These phenomena have, however, been otherwise explained. (c) Bert's experiment of fixing the end of a rat's tail in a wound on the back, and dividing the tail at its root after union had taken place, would seem to show that the stimulus is transmitted both ways in case of sensory nerves. Irritation at the root of the divided tail causes manifestations of pain, showing a transmission of the sensation in the direction opposite to the normal one, but François-Franck has referred these sensations to the phenomenon of recurrent sensibility. (d) Kühne's experiment on the double conductivity of motor nerves is done in the following way. He plunges the upper end of the sartorius of a frog into oil at 40°C. (104°F.), which coagulates the muscular substance without altering the nerves. Then, in making transverse sections of this part of the muscle from above downwards, a point is arrived at when section causes contraction to appear in the lower segment. He explains this by the irritation of a motor nerve, which is transmitted to the spinal cord, and then reflected to the periphery.

As we have seen, most of these facts will bear a different interpretation; but the balance of evidence seems to be in favor

of the theory of transmission of the nerve current in both directions from the point stimulated.

(3) *Pflüger's avalanche theory*.—Budge was the first to observe that, in stimulating a motor nerve near its muscle, a more powerful stimulus was necessary, than when a distant point was chosen; and this observation was repeated and elaborately investigated by Pflüger, who found that a current of given strength gave more marked results as the point stimulated was farther from the muscle. From this he concluded that the nerve current, in its downward passage, caused a disengagement of the forces of tension which added to its power, and, according to this view, the nerve would be not merely an organ of transmission, but a seat of disengagement of nerve-force.

Some, however, interpret the phenomena by the greater excitability of the central part of the nerve.

With regard to the results of sensory nerve stimulation, it is only known that peripheral stimulation gives better marked results than central (Cl. Bernard, Richet).

Velocity of the nerve-current.—This is incomparably slower than that of the electric current, to which physiologists usually compare it. In the case of motor nerves, it is about 33 metres per second in man, 26—27 in the frog (Helmholtz). A wide discrepancy exists in the reports of different observers as to the rate for a sensory nerve; Helmholtz makes it to be 60 metres, Richet 50, Kohlrausch 94, and Bloch 132. The velocity is diminished by cold; increasing the intensity of the stimulus increases the velocity of its transmission, and it is markedly modified by the state of electrotonus. The part of the nerve in a state of anelectrotonus gives a slower rate of transmission, and this becomes more marked as the duration and intensity of the polarising current increases (v. Bezold). When the current is very strong, the transmission is completely arrested. Catelectrotonus on the other hand, favors the transmission which is now accelerated, except for very strong currents, in which case it is arrested, as in case of anelectrotonus (Rutherford, Wundt). This paralysing action of a strong current has also been shown to exist for the inhibitory fibres of the pneumogastric.

PRODUCTION OF HEAT IN NERVES.

An elevation of temperature in stimulated nerves has been observed by Valentine and Oehl. His results have, however,

been controverted by Helmholtz and Heidenhain, but more recently confirmed by Schiff, who has shown in warm-blooded animals whose temperature has been artificially lowered, that an evolution of heat takes place in the nerves at the moment of tetanisation by induced currents.

ELECTRIC PHENOMENA OF NERVES.

Nerve-current.—In nerves as in muscles, the deviation of the needle of the galvanometer indicates a current which passes in an undivided nerve, from the transverse surface to the longitudinal. The surface of the nerve is electrified positively, the cut end negatively. The deviation of the needle is more feeble in cases of the nerve, showing the greater resistance of the latter. This nerve-current has been found to exist in all kinds of nerves, and in all animals examined (Du Bois-Reymond). The general laws which influence it are the same as those of the muscle currents already described.

The electro-motor power of the nerve current has been calculated by Du Bois-Reymond at .022 Daniel for the frog, and .026 for the rabbit. After death it gradually disappears from the centre towards the periphery, passing away sooner than the muscle-current, but lasting a little longer than the nervous irritability.

A temperature of 14° — 25° C. ($57^{\circ}.2$ — 77° F.) is most favorable to the nerve-current. A very high temperature has the effect of reversing the current, so has desiccation, and certain nerve lesions. When the current has disappeared in a divided nerve, a new section causes it to reappear.

According to Hermann the nerve-current, like the muscle-current, is merely the result of the preparation to which the nerve has been submitted, and does not exist in a perfectly healthy nerve during repose.

(b) *Induced Currents.*—In employing this form of stimulation, besides those mentioned above, an induction apparatus is necessary. That most used is the *appareil à glissement* of Du Bois-Reymond.

(c) *Condenser.*—Forms of electric condensing apparatus are employed by Marey and Siegel in preference to the others which we have noticed. The structure and application are complicated, and must be studied in the special memoirs of these authors.

Electro-capillary Currents have been used by Siegel for nerve stimulation. Mercury is allowed to flow in a vessel beneath dilute sulphuric acid,

and through a capillary tube; when a motor nerve communicates on one side with the mercury in the vessel, and on the other with that of the tube, a contraction follows the fall of each drop of mercury, and if the drops succeed one another with sufficient frequency muscular tetanus is produced.

The *Telephone* has also been employed for the stimulation of motor nerves. If a motor nerve be placed in the circuit of the telephone, and one speaks with a high voice before the plate, a muscular contraction results. Högyes has constructed, on the principle of the telephone, a magnetic inductor for the stimulation of nerves and muscles.

Modes of Stimulation.—The stimulation of a nerve may be *immediate*, (*direct*), or *mediate*. In the former the electrodes are placed in contact with the nerve, and by this method the stimulus can be exactly localised, and the point of application reduced to a minimum. In the latter the electrodes are applied with the intervention of other tissues, skin, muscle, &c.

Either of the two forms may be *unipolar* or *bipolar*.

In *bipolar stimulation*, which is the more frequently employed, the electrodes are both placed on the nerve, and at a variable distance apart. In this the nerve is traversed by a current which enters from the positive pole (anode), and leaves by the negative pole (cathode). If (in case of a motor nerve), the positive pole be nearer the nerve-centre, and the negative towards the muscle, the current passes in the same direction as the physiological motor impulse, and is called the *descending* (*direct*) current; when the position of the poles is reversed the current is said to be *ascending* (*inverse*).

Unipolar stimulation has been employed by Chauveau. A single electrode is placed in contact with the nerve; the other electrode is represented either by a large moist surface, or by a salt solution in which the nerve or other structure is submerged; or the second electrode may be placed on a distant nerve. It has been objected to this method by Hermann that at the point where the nerve enters the muscle there is a sudden variation in the density of the current, and accordingly a point on the nerve which really represents a second electrode of contrary sign.

Action of the constant current.—(*a*). *For motor nerves.*

When a constant current traverses a motor nerve, a contraction occurs only at the closing and at the opening; it is only in certain exceptional cases that there are any contractions during its passage. The opening and closing contractions appear in the following order (*Pflüger's law*, law of muscular contraction):—

Intensity of current.	Ascending current.	Descending current.
Feeble	{ Closing.—Contraction. Opening.—Repose.	Closing.—Contraction. Opening.—Repose.
Mean	{ Closing.—Contraction. Opening.—Contraction.	Closing.—Contraction. Opening.—Contraction.
Strong	{ Closing.—Repose. Opening.—Contraction.	Closing.—Contraction. Opening.—Repose.

RITTER'S TABLE (1798—1805).

Periods of excitability.	Ascending current.	Descending current.
1st period	{ Closing.—Contraction. Opening.—Repose.	Closing.—Repose. Opening.—Contraction.
2nd "	{ Closing.—Contraction. Opening.—Contraction (feeble)	Closing.—Contraction (feeble) Opening.—Contraction.
3rd "	{ Closing.—Contraction. Opening.—Contraction.	Closing.—Contraction. Opening.—Contraction.
4th "	{ Closing.—Contraction (feeble). Opening.—Contraction.	Closing.—Contraction. Opening.—Contraction (feeble)
5th "	{ Closing.—Repose. Opening.—Contraction.	Closing.—Contraction. Opening.—Repose.
6th "	{ Closing.—Repose. Opening.—Repose.	Closing.—Contraction (feeble) Opening.—Repose.

Ritter's periods of excitability correspond to the different phases which follow the section of the nerve.

HEIDENHAIN'S TABLE (1857).

Intensity of current.	Ascending current.	Descending current.
I.	{ Closing.—Contraction. Opening.—Repose.	Closing.—Repose. Opening.—Repose.
II.	{ Closing.—Contraction. Opening.—Repose.	Closing.—Repose (rarely contraction). Opening.—Contraction (rarely repose).
III.	{ Closing.—Contraction. Opening.—Repose.	Closing.—Contraction. Opening.—Contraction.
IV.	{ Opening.—Repose. Closing.—Contraction.	Closing.—Contraction. Opening.—Contraction.

The influence of the *direction of the current* was recognised, for the first time, by Pfaff (1793), and of late years elaborately investigated by Ritter, Heidenhain, Cl. Bernard, and many others; but Pflüger has the merit of tabulating, with great precision, the influences of the different intervening conditions.

A muscular contraction is produced, not only by the opening or closing of the current, but by every sudden variation of

intensity, or still more of the density of the current (Du Bois-Reymond, Cl. Bernard). In the case of the living animal, it has been found that, whatever be the direction of the current, the closing contraction is more powerful than the other, and sometimes is the only one to appear (Cl. Bernard, Schiff). The researches of Fick on man have given the same results, but Brenner, by using stronger currents, confirmed Pflüger's law in case of man.

Pflüger has applied these facts to his own law, and sought to interpret the latter by their aid. We have seen that the stimulating action of a current is produced, at the closing of the current, at the cathode only; at the opening, at the anode

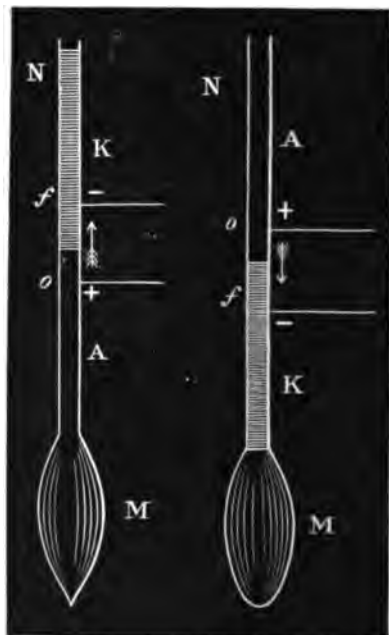


Fig. 44.

Diagrams illustrating the law of Pflüger; ascending current on left, descending current on right side. M, muscle; K, catelectrotonic portion of nerve; A, anelectrotonic part; o, anode; f, cathode; the striated part represents the increase of irritability.

only : in other words, the nerve is excited but by the onset or increase of the catelectrotonus, and (to a much less degree) by the disappearance or diminution of anelectrotonus. In case of an ascending current, the closing causes stimulation of the upper part of the nerve, and opening stimulates the lower part ; the reverse is the case for the descending current. Besides, electrotonus modifies not only the irritability of a nerve, but also its capability of transmitting a stimulus, so that the part of the nerve, in a state of anelectrotonus, offers a greater resistance to the passage of a stimulus, and this resistance increases with the duration and intensity of the polarising current.

We are now in a position to interpret the laws of Pflüger :—

(A). *In case of an ascending current.*

(1). *If the current be strong*, the anelectrotonic part of the nerve loses its conductivity ; the stimulus of the closing is not transmitted to the muscle, and no contraction follows. At the opening of the current, on the contrary, the anelectrotonus disappears, stimulation is produced at the anode, and the muscle contracts.

(2). *If the current be a medium one*, the conductivity of the anelectrotonic part is not affected, and the stimulation produced at the opening and closing of the current is transmitted to the muscle, which contracts in each case.

(3). *If the current be very feeble*, the stimulation is only effective at the point furthest from the muscle, and the closing produces contraction.

(B). *For the descending current.*

(1). If the current be a strong one, the stimulus of closing produces a contraction ; but the stimulation of opening, acting on the anelectrotonic part, has no such effect.

(2). If the current be of medium strength, contraction takes place at the opening and closing of the current, for the same cause as in case of the ascending current.

(3). If the current be very feeble, there should occur a contraction at the opening of the current, as it is the stimulation of the point more distant from the muscle which determines the contraction ; but, because the onset of the catelectrotonus is a more powerful stimulant than the disappearance of the

anelectrotonus, the effect of the latter is too slight to give any manifest result.

The law of Pflüger, in all its phases, may be expressed by the following general formula :—*Irritation of a nerve is manifested as soon as the external forces come to change, with a certain degree of rapidity, its internal molecular constitution.* The static condition of a nerve is never accompanied by any evidence of irritation.

In case of sensory nerves, it was found by Marianini (in the frog), and by Matteucci (in the rabbit), that, for a descending current, closing produced contraction and breaking caused pain, while, in case of ascending currents, pain was manifested at the closing and contraction at the opening. The experiments of Pflüger confirmed the results of Marianini and Matteucci in case of very strong currents ; for currents of medium strength contraction occurred with all four modes of stimulation (both opening and closing in either direction of the current) ; when the currents were very feeble, the results were so irregular that no definite conclusion could be drawn. So that it may be said, as a general rule, that the law of Pflüger applies to sensory nerves as well as to motor. Pflüger's experiments on the vagus have given the same results for inhibitory nerves.

Influence of length of nerve.—For currents of equal strength, the result is greater (the muscular contraction stronger) as the length of nerve traversed by the current increases.

Influence of the direction of the current with regard to the axis of the nerve.—To produce stimulation by a nerve current it is necessary that the rheophores should be placed at a certain distance apart. When placed one opposite the other, so that the current passes through the nerve transversely, no evidence of stimulation follows, be the current ever so strong (Galvani). This fact, more recently demonstrated by the experiments of Albrecht and Meyer, is explained by the neutralising effects of anelectrotonus and catelectrotonus of the opposite poles.

Influence of the duration of the current.—To produce nerve-stimulation it is necessary that the constant current should have a certain duration (.0015 sec., according to Kœnig) ; without this electrotonus cannot be established. For the breaking contraction a longer duration is necessary than for the closing contraction ; the anelectrotonus, of which the disappearance produces the breaking contraction, is slower to

produce than catelectrotonus. When the continued current undergoes very rapid interruptions their action is identical with that of the induced current. After death, or after exposure to cold, a longer duration of the current is necessary to produce a definite result.

Tetanus produced by constant currents.—This phenomenon has been observed by Du Bois-Reymond, Chauveau, and Pflüger. The continuation of the contraction during the whole time of the passage of the current, had been attributed to the electrolysis produced, but this is not a satisfactory explanation (Pflüger). This tetanisation is produced by feeble currents ; it increases at first with the intensity of the current, and subsequently diminishes ; it is more pronounced with the descending current, and increases with the length of the stimulated nerve. The vaso-dilator nerves of the skin are, according to Grützner, the only ones permanently excited during the passage of a constant current.

The same phenomena have been observed in case of sensory nerves. The passage of a constant current along a sensory nerve produces pain, not only at the time of opening and closing, but during the whole time of its passage.

Negative variation of the nerve current.—If a piece of nerve be placed in the galvanometric circuit, the deviation of the needle indicates the existence of the nerve-current already described, so long as the nerve is at rest. When the nerve is tetanised, the needle is seen to turn back towards zero, and sometimes even passes the latter. It occurs in all kinds of nerves, and in the whole extent of the nerve. It is not an electric phenomenon, due to this variety of stimulation, for it is seen on application of chemical or mechanical stimuli ; while its appearance is prevented by placing a ligature on the nerve, which does not prevent the electric conduction. The negative variation increases with the intensity of the stimulus, but there is not a definite proportion between them ; it is greater when the stimulated point is in a state of catelectrotonus, less when that point is in anelectrotonus.

For a single application of the stimulus, there is no deviation of the galvanometer needle ; if very delicate instruments are used, there is found to be an excessively brief negative variation, and the negative variation of a nerve in tetanus is made up of a series of negative variations corresponding in number to the

stimuli applied. The appearance of the negative variation is preceded by a latent period of $\frac{1}{1450}$ sec. (Bernstein).

According to Hermann, the negative variation is the expression of a special current, the direction of which is contrary to the current of repose, and to which he gives the name of *current of activity*. It is due to the fact that the stimulated point of the nerve behaves itself negatively with regard to all the other points.

Electrotonic phenomena of nerves.—Du Bois-Reymond was the first to show that when a constant (polarising) current was passed along a living nerve, in the same direction as the proper nerve current, the latter was strengthened (*positive phase of electrotonus*); but when the polarising current was passed in the opposite direction, the nerve current was weakened (*negative phase of electrotonus*). These changes were not limited to the intra-polar part of the nerve, but passed on each side to the two extremities. The law of the phenomenon can then be formulated in the following way:—When a polarising current traverses a segment of a nerve, all the other points of the nerve are traversed by a current in the same direction, which is added *algebraically* to the nervous current of repose, when the latter exists.

The electrotonic currents are then independent of the ordinary nerve-currents; their intensity increases with the intensity of the stimulant, and also with the length of the nerve traversed by the polarising current. They are stronger near the intrapolar region, and the electro-motive force may reach that of .5 (Daniell), which is much higher than the proper nerve-current (Du Bois-Reymond). The electrotonus is stronger at the anode than at the cathode, and is not seen if a ligature has been placed on the nerve, or if it has been fatigued by strong currents, nor if developed under the influence of mechanical or chemical stimuli. When a nerve is tetanised, which has already been thrown into a state of electrotonus by a polarising current, the electrotonic current, like the nervous current of repose, undergoes a negative variation.

THEORIES OF NERVOUS AND MUSCULAR ELECTRICITY.

Two theories have been advanced for the explanation of these phenomena: the *molecular theory* of Du Bois-Reymond, and Hermann's *theory of alteration*.

(1). Du Bois-Reymond supposes that every muscular or nervous fibre is made up of an infinite number of small electro-motive elements, each consisting of an equatorial positive zone and a negative polar zone, and placed in an interstitial conducting substance. The arrangement in a muscular or nervous fibre is represented by the following diagram :—

— + — — + — — + — — + —

The relations remain unchanged, if we suppose each of these elements divided into two tripolar molecules, of which the positive poles are turned towards one another, and arranged in the following fashion :—

— + + — — + + — — + + — — + + —

Fig. 45 represents the disposition of the bipolar molecule in muscle ; the arrows indicating the direction of the current

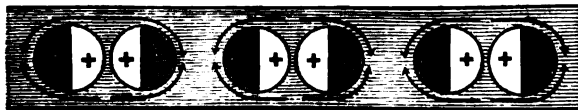


Fig. 45.

in the interstitial substance (Funke). To explain the phenomenon of electrotonus Du Bois-Reymond considers that the molecules undergo the change of order indicated in Fig. 46.

To explain the phenomenon of parelectronomus he supposes that at each end of the muscle is found a single row of tripolar



Fig. 46. Bipolar elements in electrotonus (after Funke).

molecules, of which the positive pole is placed next the tendon.

they are explained by admitting that, during stimulation, the active parts are negative with regard to the parts at rest.

Chemical theories.—Liebig was one of the first to suggest that the muscle current was due to the difference in reaction between the circulating blood (alkaline) and the muscular tissue (acid). Ranke, by observing the difference in the behaviour of the various anatomical elements with the picro-carminate of ammonia, found that the nucleus of cells was acid, with regard to the cell-contents; that the axis-cylinder was acid in relation to the nerve-sheath, and the interstitial substance of muscle with regard to the sarcous elements. This led him to believe that all the anatomical elements are electro-motor, and that multiple electric currents are continually being prepared in the organism. E. Becquerel has demonstrated that electro-chemical circuits may exist without the intervention of a metal; the presence of two liquids of different nature, separated by a membrane or by a capillary tube, being all that is necessary. The wall in contact with the liquid behaves as the positive pole, the opposite wall forms the negative pole; while the walls of the capillary spaces form solid conductors. In this way there is an incessant development of electro-capillary currents, which disappear only after death. These electro-chemical changes not only explain the muscle and nerve-currents, and those of bone (demonstrated by E. Becquerel), but also the exchanges which take place between the blood in the capillaries and the surrounding tissues.

Fatigue of nerves.—Great difficulties lie in the way of estimating the degree of exhaustion produced in nerves by prolonged stimulation. It is usually observed in connection with muscular contraction, and it is then almost impossible to determine how much of the alteration is due to the change in the muscle, and how much to that of the nerve. The observation made by Du Bois-Reymond, that the negative variation becomes weaker after a number of stimulations proves, however, that nervous fatigue has an existence separate from muscular fatigue. Bernstein, by passing a current across a nerve which touches a muscle, prevents the transmission of stimuli from the upper part of the nerve to the muscle. He then tries the irritability of the nerve with a fresh piece of muscle; in this way he has found that the nerve is not so soon fatigued as the muscle, and also that its irritability is more slowly re-established.

II.—PHYSIOLOGY OF THE NERVE-CELLS.

These structures are grouped in two principal forms : (*a*) in the grey matter of the brain and spinal cord ; (*b*) in the various ganglia (sympathetic chain, posterior roots of spinal nerves, &c.). In former sections enough has been said of their chemistry and physics. The grey nerve substance which contains them is distinguished by greater vascularity, more active nutrition, and more intense vitality.

Irritability of nerve-cells.—The irritability is under the immediate dependence of the general nutrition of the nerve-cells, and of all the organic conditions which determine it, especially the circulation. The irritability appears more variable than that of muscle, presenting changes more pronounced in species, races, age, sex, &c. It is increased by hyperæmia, or increase of blood-pressure ; and, on the other hand, it is increased by anæmia. Everything that increases the excitability of the peripheral nervous apparatus acts in the same way ; the presence of oxygen, of compressed air, and of certain poisons (strychnia, brucia, &c.) have the same effect. It is diminished, on the other hand, by the interruption of the circulation, as in Steno's experiment ; by fatigue, by the action of certain substances, such as the bromides, the various anæsthetics, hypnotics, narcotics, &c. The activity of some nerve-currents is also brought to a stand-still by that of some others (inhibitory centres).

There are the best reasons for believing that every manifestation of activity of nerve-cells, as of nerve-fibres, is preceded by the application of a stimulus. In most instances this is peripheral, being transmitted along the sensory or special-sense nerves ; or the motor stimulus may come from a psychical centre, as in case of voluntary movement.

In addition to the ordinary physiological stimuli, there are others less frequent and more obscure in their nature, such as those determined by a sudden afflux of blood, causing convulsions, &c.

Spontaneous action (*automatism*) of certain nerve-centres is admitted still by some physiologists of high authority. Such centres are called *automatic*, but their number is progressively diminishing, as physiological research advances.

Activity of the nerve cells.—This is manifested in two ways : in the disengagement of nerve force, and its transmission.

(a). The *transmission* of nerve force, although more especially the function of nerve fibres, is also manifested by the ganglionic cells of the nerve centres ; but appears to be less rapid in the latter situation than in the former.

(b). The *disengagement* of nerve-force is the special function of nerve-cells ; each cell is a laboratory in which nerve force is constantly being produced, and some mysterious molecular movement, the nature of which still remains unknown, causes the *discharge*.

The first striking characteristic peculiarity of a nervous discharge is its instantaneous quickness. It lasts but an inappreciably short space of time ; so that the activity of a nerve cell when it lasts for some time, is found to be intermittent, being made up of a number of successive discharges, separated by intervals of repose. In case of a motor centre, we have already seen that the discharges sent along the nerves to the corresponding muscle succeed one another so rapidly that the shocks are united to make a single total contraction. When, on the other hand, the discharges do not succeed one another with sufficient rapidity, as in the changes produced by age, and sometimes by other causes, the muscular shocks are too widely separated to be fused into one contraction, and a series of partial contractions result, as in senile or alcoholic tremors.

The same intermittent action is probably present in the other nerve centres, and a peculiar form of this functional activity is seen in the *rhythmic character* of some forms of nervous action ; the movements of the heart, respiration, &c. A still more remarkable manifestation of the intermittence of nervous activity is seen in the alternation of sleep and wakefulness.

The intensity of the nervous discharge varies according to certain conditions, which are imperfectly known. As a general rule it increases with the intensity of the stimulant.

A peculiar characteristic of the action of the nerve-centres is the tendency of a certain nervous movement, frequently repeated, to reproduce itself more easily on slight stimulation. If it is a motor nerve-centre, the movement becomes, as it were, mechanical, and causes a certain amount of uneasiness if restrained. Similarly, in case of sensory nerve-centres, the ces-

sation of an accustomed stimulant causes an ill-defined sensation of desire (*besoin*).

Every stimulation of a nerve-cell leaves, after the manifestation of its activity, a certain modification which lasts for a longer or shorter time.

The phenomena of fatigue are manifested by nerve-cells as by muscle tissue. Certain substances produce nervous exhaustion, and, as in case of muscle, the products of disassimilation of nerve-tissue act in this way (Ranke).

Classification of nerve-centres.—The following classification of nerve-centres is made by Beaunis :—

(1). *Centres of impression* : these receive the various impressions which are conveyed from a distance (tactile sensations, the various special sense impressions, &c.) ;

(2). *Centres of action* : these include motor, secretory, &c.) ;

(3). *Centres of psychical action* (perception, ideation, volition, &c.) ;

(4). *Centres of inhibition* : the activity of which manifests itself by the diminution of that of other centres, especially motor.

III.—PHYSIOLOGY OF THE PERIPHERAL NERVE-ORGANS.

The peripheral nerve organs may be looked on as true commutators of movement ; the end-plates of voluntary muscle transform the molecular movement produced in the nerve and transmit it to the contractile substance of the muscle.

The sensory peripheral organs have the peculiarity that they are influenced by stimuli, which produce no effect on ordinary nerve fibres. The manifestations of luminous or auditory impressions are probably due to the greater instability of the peculiar cellular structures found in the organs which are set apart for the reception of these peculiar impressions.

The peripheral nerve-organs have, accordingly, the special peculiarity of acting under the influence of certain determinate stimuli. This class of stimuli receives the name of *homologous* : while *heterologous* stimuli are those which act similarly on all nerves (such as chemical and mechanical agents, electricity, &c.).

IV.—GENERAL PHENOMENA OF INNERVATION.

The phenomena of innervation may be ranged under five heads: (1) impressions and sensations; (2) reflex actions; (3) instinctive acts; (4) psychical acts; (5) inhibitory actions.

A.—Impressions and Sensations.

Impressions may or may not be perceived; and by some writers on the subject the name of impressions is limited to the latter group, while the former class are distinguished by the name of sensations.

An *impression* is always followed by a reflex action, and we cannot determine its existence but by the consequent reflex act, which, in the absence of perception, shows us the intervention of the nervous system. The name of impression is not given to a form of stimulation which is limited to the point affected. Impressions are probably completely limited to the organic and vegetative functions. The contact of food with the coats of the stomach, causing a flow of gastric juice, is a good example.

Sensations (conscious impressions) are called forth either by peripheral stimulation (sensations properly so-called), or by stimulation of the nerve-centres (emotions). They may be *external*, as in the special functions of sight, hearing, touch, &c.; or *internal*, as in the feelings of hunger, thirst, &c.

Emotions are sensations of a very complex nature, characterized by their indefinite position in time and space. They probably call into play a large number of psychical centres.

B.—Reflex Action.

Taken in the widest sense, the term reflex action includes all the acts which follow stimulation of a sensory nerve; according to Rouget, it is *an impression transformed into action*. The transformation takes place in a nerve-centre, a *reflex centre*.

It had long been known that decapitated frogs executed spasmodic movements when the skin was irritated; and Hales established the fundamental principle of reflex action, when he showed that such movements ceased on destruction of the spinal cord. Prochaska was the first to make it a matter of

real scientific study ; and Marshall Hall found that this peculiar form of action was not limited to the spinal cord, but found another example in the separated head, where touching of the eye-ball caused closing of the eyelids, a movement which immediately ceased on destruction of the brain.

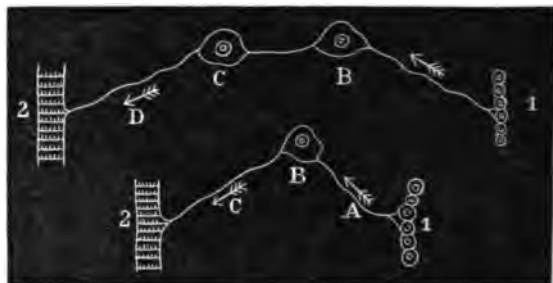


Fig. 47. Single and double arcs.

The simplest type of reflex movement consists of three phases : (1) initial stimulation of a sensory nerve ; (2) stimulation of an intermediary nerve-centre ; (3) stimulation of a motor nerve and the reflex movement which accompanies it. The sensory and motor nerves, with the connecting centre between, form a *nervous arc*. The nervous or excito-motor arc (see Fig. 47; A B C) is all that is necessary. The primary stimulus is applied at (1) and conveyed along the sensory nerve to the centre B, from which it passes into the motor nerve-fibre C, which conveys it down to the muscle. The change of direction, which the nervous stimulus undergoes at the nerve centre, has been compared to the reflection which a ray of light undergoes when it falls obliquely on a mirror, and hence the name applied to it.

A reflex nerve centre is usually formed by two nerve cells, a sensory and a motor, united by a commissural fibre.

With regard to the different phases, the following features have been observed :—

(1). The *initial stimulation* may come from any sensory nerve, whether of special sense, tactile sensation, or visceral ;

there are, however, some which produce more active reflex movements, among which may be mentioned those of the palm of the hand and sole of the foot. The nature and quality of the stimulus applied influences the resulting reflex; tickling the meatus auditorius externus produces cough, while simple contact has no effect; and, as a rule, the movement produced corresponds exactly to the stimulus employed.

Reflex action follows stimulation of a sensory nerve-trunk in any part of its course, but the movement in the latter case is much more energetic, and its character is manifestly altered; for, in such a case, the stimulation causes movement in one or more muscles, while stimulation of the cutaneous surface supplied by the same nerve produces movements which have a peculiar character of co-ordination (Fick).

In order to produce reflex action, the application of the stimulus must be sufficiently rapid; anything that produces a slow and gradual change in the nerve has no effect. Setschenow has found a difference between the reflex of chemical and that of mechanical stimulation; and Danilewsky distinguishes *tactile* reflexes from the *pathic* produced by painful applications.

(2). The *stimulation of the reflex centres* produces greater or less results, according as the centre possesses greater or less irritability; this property being influenced by the same conditions which govern that of the nerve-cells, and which we have already considered. We have also seen that every centre which gives origin to a motor nerve may be looked on as a reflex centre; and, in addition to these, there are good grounds for including among the reflex centres, the ganglia of the sympathetic system, and the grey matter of the cortex cerebri.

The excitability of the reflex centres is increased when their communication with the psychical centres (especially those which preside over voluntary movement) is cut off, or when the latter centres remain inactive. Accordingly, after decapitation, removal of the brain, section of the bulb, or medulla spinalis, the reflex movements dependent on the centres below the lesion are greatly intensified. This result may be attributed to the presence of inhibitory centres, which in the normal condition control the excitability of the reflex centres (Setschenow).

Reflex excitability is much greater in young animals than in adults; this accounts for the readiness with which slight causes

produce convulsions during infancy. It is greatly increased by the ingestion of certain substances, especially strychnia, so that in an animal poisoned by strychnia the slightest touch brings on convulsions. It is diminished by atropin, bromides, &c. It is generally more pronounced in summer than in winter, although some observers have found it increased by lowering the temperature (Archangelsky, Tarchanoff, Wundt, &c.).

The time occupied in the nerve-centres, by the transformation of sensation into motion (*duration of the reflex transmission*) has been measured by Helmholtz, Baxt, and others. It is calculated by deducting from the total period that elapses between the application of the stimulant and the reflex contraction the time necessary for its transmission along the nerve fibres.

(3.) The reflex movement, which is the third phase of reflex action, is the *necessary* consequence of stimulation of a reflex centre, and is, accordingly, entirely beyond the control of the will. These movements are seen in both kinds of muscle, the smooth as well as the striated.

When a reflex movement engages a number of muscles, or groups of muscles, we have compound reflex movements, which are made up of a number of simultaneous or successive reflexes. When these are co-ordinate, they cause a definite action, such as we see in coughing.

Pflüger's Law of Reflexes.—The way in which a simple reflex contraction may be converted into a compound movement is diagrammatically shown in the accompanying figure. When the skin of one of the hind-legs (P) of a decapitated frog is irritated, the stimulus is transmitted to the centre (A), and reflected from it to the muscles (1) of the same limb (*law of unilaterality*). When the stimulus is somewhat stronger it is reflected to the opposite side (B), and contraction of corresponding muscles (2) on that side (*law of symmetry*) appear, although less strong than those on the other. When the stimulus is increased still more it reaches the higher centres (C, D), and causes movements in the upper limb, first on the same side (3), and afterwards on the opposite side (4) (*law of irradiation*). At last the stimulus, always increasing in intensity, arrives at the main reflex centre (E) (in the bulb), which presides over the movements of nearly all the muscles,

and general convulsions follow (*law of generalisation of reflex movements*).

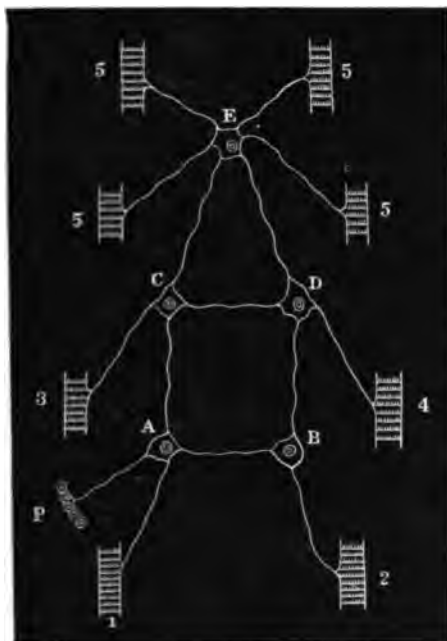


Fig. 48.

The reflex centres are superposed in graduated form so as to preside over larger and larger groups of muscles, as represented diagrammatically in Fig. 49. The cell (1), for instance, presides over the contraction of the muscle M. The three first muscles are under the control of a higher cell (2), so that if it be stimulated all three contract simultaneously, while, if the inferior cells (1) be stimulated, they contract singly. The cell (3) again presides over the contractions of two groups of muscles, and consequently over much more complex movements; so that if the cells (2) preside, the first over flexion of

the leg, and the second over flexion of the thigh, the cell (3) which commands both these has under its direction the two movements which, taken together, form a step in walking, while the cell (4) which is still higher in the scale would

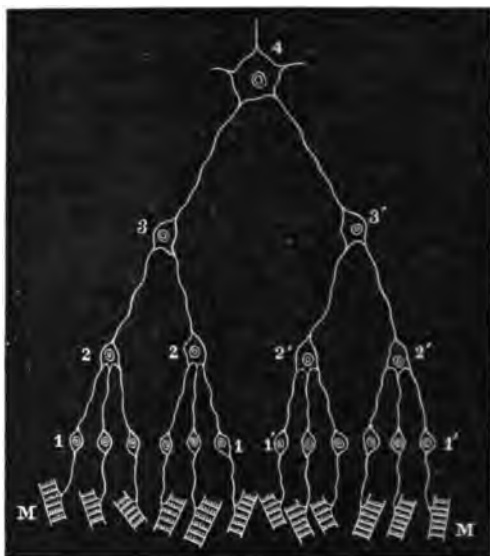


Fig. 49.

preside over all the movements which have to be thrown into co-ordination in walking. The same things may be said of all compound reflex movements, and an initial stimulation of the periphery, acting on the single superior centre, suffices for the production of all the compound groups of reflex movements over which this centre presides.

Some compound reflex movements appear to be innate, such as that of suckling in the infant; while others are developed by habit and exercise, such as that of walking, which has been known to be done by wearied soldiers sleeping on the march, although, as we know, the difficulty of learning the habit in

early life is very considerable indeed. The automatism of some movements, which at first require voluntary effort and attention, is obviously connected with a gradual modification and approach to perfection in the structure of those nerve-centres which preside over such movements. This adaptation of function seems to become hereditary in the succession of generations, and with it increased aptitude for the performance of such movements; and, as in the life of the individual, movements which were at first voluntary become mechanical by prolonged exercise, so the voluntary movements of parents may become mechanical and automatic in their descendants, in the course of many generations.

The so-called *automatic* movements are but a variety of reflex actions, which are *rhythmic* in succession (such as the movements of the heart, those of respiration, &c.), and of which the seat of initial stimulation is difficult to localise.

Reflex Secretion.—Reflex action is seen in connection with glandular surfaces giving rise to a sudden increase of their secretion; and the activity of all, or nearly all, of the glands is found to be influenced in this way. The stimulus may be either central or peripheral, and we shall see examples of each form when we come to deal with the physiology of the various secretions.

Reflex Sensations.—Formerly certain obscure sensations, such as those of muscular fatigue, were referred to reflex action. But this sensation can be satisfactorily explained by the presence of sensory nerves in muscle. There are some associated sensations which are harder to explain, such as the tickling sensation in the nose when we look at the sun.

C.—Instinctive Acts.

These are after all but complicated automatic acts, or are groups of automatic acts co-ordinated for a certain end. According to this theory, instinct is but a reflex phenomenon of more complex order than the ordinary reflexes, and the co-ordination is so pronounced that acts of this kind approach psychical acts. The most striking examples of these are seen in the incubation of birds, in the political economy of the life of bees, ants, &c.

The initial stimulation which determines acts of this kind is

often extremely obscure, but in a large proportion of cases it must be central; emotions, desires, and internal sensations of various kinds are oftenest the physiological stimulants to instinctive acts; such as we see produced by hunger, fear, maternal love, sexual sensations, &c.

The localisation of the centres of the instinctive acts still remains undetermined. They must probably be placed above the automatic centres, and consequently in the higher parts of the nervous axis, but no further approach to certainty has been arrived at.

Applying to those acts the process of reasoning we have already adopted, it is very probable that the so-called instinctive actions were all originally voluntary and intelligent, and that, in consequence of constant repetition and hereditary succession, they end by becoming involuntary and instinctive.

D.—Psychical Actions.

These are the most complex and difficult to analyse of all nervous actions. The following are the chief general conclusions that have been determined about them:—

(1). The activity of the psychical nerve-cells is always accompanied by consciousness. Nevertheless this assertion cannot be received without qualification, for on account of force of habit and simultaneous multiplicity of psychical acts, many are unperceived, and those only excite our attention which surpass in their intensity or some other prominent feature. Accordingly the law above enunciated would be perhaps better expressed in the following terms: the activity of psychical nerve-cells is conscious only when it reaches a certain degree of intensity.

(2). The psychical nerve-cells have the power of preserving for some time the modifications produced by the influence of the stimuli which excite them. Accordingly, mental impressions persist for some time before being effaced; and this phenomenon has been compared by Luys to the phosphorescence of inorganic bodies, or to the peculiar power of retaining light which was observed by Niepce de Saint-Victor in engravings exposed to the solar rays, and which, after being kept in darkness for twenty-four hours, were still able to impress a sensitive plate. The modification so produced in the nerve-

cell may long exist in the latent state without our being conscious of it ; and it exists, not only for impressions, but for movements and for ideas.

(3.) A modification once produced, and persisting in a psychical nerve-cell in a latent state, may, under certain circumstances, re-appear with sufficient intensity to be perceived and to give rise to psychical acts. This property has received from some writers the name of *reviviscence*, and is the one on which memory depends.

(4.) When two successive modifications of the same nerve-cell are produced, we are conscious not only of both, but also of their difference and resemblance.

(5.) A modification produced in a nerve-cell is able in turn to act as initial stimulant to other nerve-cells of the same or of a neighboring group, and they act in preference on the cells which have been frequently excited at the same time as themselves, or soon after them. On this property depends the associations of ideas, of movements, of remembrances, &c. ; and these associations are so strong that they are produced even against our will.

(6.) Whether the psychical cells are possessed of *spontaneity*, and so differ from all other varieties of nerve-cells, is a question among authorities on this subject, many of whom have answered in the affirmative. But this is a conclusion which we should be slow to accept finally, knowing the great peculiarity of other cells, and the difficulty of discovering the initial stimulus, even in many of those cases in which we feel sure that such exists.

We have already seen that, with regard to minor cells, there exists a kind of hierarchy from those which govern a single muscle to those presiding over a complex combination of movements, such as walking ; and, in case of the psychical centres, we find a similar form of government, from the inferior cells, which receive the rough impressions from sensory surfaces, to the superior cells which perform the most complex operations of the human intellect.

Of the peculiar properties of these cells, one of the most important is the power of fusing together the sensations received by several inferior cells. This may be exemplified by taking the instance of a solid body, such as a stone : the stimulation of the retina by the luminous vibrations from this body is transmitted to the nerve-centre and produces a certain

visual sensation corresponding to the form ; touching the stone causes a peculiar modification of another nerve-centre, giving rise to *tactile sensation* ; while pressing against it, or lifting it from the ground, causes another sensation differing from the others—the so-called *muscular sense*. These three sensations are transmitted to a higher centre, with which they are all connected, and by which they are fused together so as to give rise to a definite idea of an object which we have seen, touched, and palpated. This is the first step in the process of *generalisation* and *abstraction*, and as the stimuli are transmitted successively nearer to the higher centres, the notions formed become more and more generalised, till we at last come to the highest generalisations of time, space, and motion.

A second peculiar property of the superior psychical centres is the recognition of *co-existence* and of *succession*, the being able to tell whether two stimuli which affect the nerve-centre act simultaneously or successively. There are, however, limits to this power, and we shall see that, in the study of special sensations, when two sensations succeed one another very rapidly they seem to be one.

E.—Inhibitory Actions.

Some nerve-centres appear to act, not as stimulants to muscular action, but as bridles. The first known example of this peculiar action, and the one which has been most studied, is that of the pneumogastric on the heart, which we have already described at sufficient length.

With regard to the different *theories of nervous action*, it must be confessed that the peculiar influence manifested by the nervous system on the other parts of the body remains almost as obscure to us as it was to the ancient physiologists. Accordingly it must be useless to discuss the subject in an elementary work on physiology.

CHAPTER X.

INNERVATION.

TACTILE SENSATION.

Tactile sensations are produced by mechanical actions, contact, pressure, traction, &c. The stimulation so caused is conducted to the nerve-centres by the sensory nerves of the skin and mucous membranes. The mode of application of a mechanical stimulus differs according as the body is solid, liquid, or gaseous.

(1) *Solids*.—These act either by pressure, or by traction. *Pressure* may vary from zero to a maximum, which has no limit but the disorganization of the tissues. Up to a certain minimum, which depends on the sensibility of the region, the application excites no sensation. The minimum pressure corresponds to the sensation of simple *contact*; this, by degrees, gives way to the sensation of *pressure*, and when the pressure is sufficiently increased it gives place to *pain*, and this, in its turn, disappears when the pressure is increased to disorganization of the tissues.

Pressure varies not only in *intensity*, but in *extent*; and however the latter may be limited, the pressure always affects at least more than one peripheral nerve-ending. The pressure may be *uniform*, when it is equally distributed over the different points of the surface touched; or, as usually happens, it is *irregular*, when the tactile sensations are much more clearly defined. This is seen when a rough body touches the skin; it meets the latter in a number of points leaving intervals untouched between, and gives a much more vivid sensation than a smooth body which touches the skin over a vast number of points; and, in fact, *irregularity of pressure seems to be an essential in tactile sensation*. This is probably the explanation of the physiological use of the papillary ridges of the finger and hand, where the tactile sensations are most highly developed.

When the tactile sensations are very light (*frôlement*), and succeed one another rapidly, a large number of nerve fibres are stimulated, and the sensations excited produce a peculiar sensation (that of *tickling*).

Traction (on the hair, nails, &c.), determines the sensation of pain much more rapidly than does pressure, and the sensitive scale is much more extended than for the sensations caused by the latter.

(2) *Liquids*.—Liquids (applied at the temperature of the skin) exercise a uniform pressure on all points of the cutaneous surface, excepting those at the level of the surface of the fluid. If a finger is plunged in a heavy liquid, such as metallic mercury, the part submerged bears a pressure which decreases uniformly from below upwards; it is only at the surface of the liquid that a marked inequality of the pressure exists, following a circular line which surrounds the finger at this level. If a lighter fluid (such as water) be used, the pressure sensation is but very slight.

(3) *Gas*.—A current of air or other gases which strikes the skin with some velocity causes a tactile sensation, and this is much more pronounced when it strikes the surface obliquely.

The mode of transmission of mechanical stimulations to the sensory nerves is not clearly understood. The structure of the nerve-endings will be described later on, when we come to describe the structure of the skin itself; they are: the *Pacinian corpuscles*, the *end-bulbs* of Krause, and the *corpuscula tactus* of Wagner and Meissner. Besides these a delicate plexus of non-medullated nerve-fibres has been described by some authorities in the rete Malpighii. A very slight pressure is probably sufficient to reach these structures, with the exception of the Pacinian corpuscles, which are situated beneath the true skin. Whether mechanical stimulation affects the structures by simple pressure, or by causing a series of vibrations which act upon these nerve-endings, in a manner analogous to the vibrations of air on the auditory nerve, or of light on the retina, is a question which has been often asked, but still remains unanswered. The horny layer of the epidermis is the structure which first receives the pressure from without, and its presence serves to protect the nervous filaments; if it be removed, all tactile sensation gives place to pain, while, at the same time, precision is completely lost. The more yielding

rete mucosum, elastic and semi-fluid in consistence, transmits the mechanical stimulation to the terminal nerve-organs. Krause believes that he finds in the corpuscles peculiarities of structure which tend to increase the pressure in the central parts; and Meissner considers that the disposition of the nerve-fibres in the corpuscles described by him distinctly favors the transmission of oscillations, to which he would refer tactile sensations.

In the recent experiments of Tschiriew and de Watteville, the electric excitability of the cutaneous nerves has been found to be the same over the whole surface of the body. This disproves the results of the less elaborate investigations formerly made on the subject by Munk, Leyden, Drosdoff, &c.

Tactile Sensations are of two varieties: sensations of *pressure*, and sensations of *traction*.

(1) **Sensations of Pressure.**—The sensations of contact and of pressure are but different degrees of the same feeling. Still they seem to reside in different anatomical structures. The sensation of contact seems to reside in the tactile corpuscles; it is abolished in cicatrices after the destruction of the papillary layer of the cutis; the sensation of pressure still persists, and seems to depend on the Pacinian corpuscles, which lie in the subcutaneous areolar tissue.

(2) **Sensations of Contact.**—These may vary in *intensity*, in *nature*, and in *extent*.

The variations of *intensity* are very limited; a very slight augmentation of the mechanical cause brings on the sensation of pressure. It is specially marked for solid bodies, and for these we may say that the sensation of contact is one and invariable in degree.

The sensation of contact varies in its *nature* according to the body. We are all familiar with the various sensations excited by touching a piece of metal, of wood, or other hard body; also that of touching a fluid, or the contact of a jet of gas, and the varying sensations have been aptly compared to the varying timbre of sound. This variety of sensations is still more striking in mucous membranes. When two parts of the cutaneous surface come into contact, the more sensitive feels the other; if a finger touches the skin of the forehead the former feels the latter, but if the finger rapidly rubs the forehead, the sensation is found to be reversed.

The *extent* of the surface of contact increases the intensity of the sensation. The minimum weight necessary to develop this sensation varies according to the region, but is hard to determine. The following table (from Aubert and Kammler) gives the minimum for some parts. The weights are in milligrammes, and press on nine square millimetres of the cutaneous surface.

Forehead, temples, nose, cheeks	2 mgrs.
Palm of hand	3 "
Eyelids, lips, abdomen	5 "
Palmar surface of index finger	15 "

The weight may be applied directly to the surface, or a balance may be employed of which the surface is furnished with a pivot which presses on the skin (Dohrn), or an elastic tube may be used which is filled with water and submitted to graduated pressure (Goltz, Bastelberger).

Speaking generally, the sensation of contact becomes less delicate as we pass from the fingers to the trunk; it is more acute on the palmar surface than on the dorsal, on the radial than on the ulnar side of the upper limb, on the left than on the right.

Sensation of Pressure.—This succeeds the one just spoken of, but it always presents a scale of intensity much larger than does the other; there are innumerable degrees before it is changed into the feeling of pain. On the other hand, there is much less variety of the characters of roughness, smoothness, &c., &c., than that of contact. The characteristic feelings excited by all bodies—wood, metal, flesh, &c., are all merged into one when the pressure becomes sufficient. The extent of the region pressed diminishes the intensity of the sensation, and also makes it less clear.

The minimum of pressure necessary to produce the sensation varies in different regions, and similarly for the maximum (beyond which the sensation of pressure gives place to pain).

For the purpose of investigating these sensations, Beaunis has devised an *asthesiometric needle*, which is suspended vertically over the skin, with a plate attached which receives the weights. The latter is lightly suspended by means of a cord, which passes over a pulley attached to the framework of the stand. Eulenberg has constructed, on the principle of the

ordinary balance, an instrument which he calls the *baræsthesiometer*.

(2) **Sensation of Traction**.—These pass through the same phases as the pressure sensations: contact, traction, pain. The sensation of contact lasts but a very short time, it rapidly passes into that of traction, which, in turn, soon gives place to pain.

(3) **Tactile sensations of mucous membranes**.—These, where they exist, are of the same nature as those of the skin, but they are limited to a part of the mucous surfaces. Some of the latter possess no tactile sensibility, such as those of the trachea, bladder, &c., while others are possessed of exquisite sensibility, even surpassing that of the skin, such as the tip of the tongue. The tactile sensibility of many of the mucous surfaces is peculiar, as that of the conjunctivæ, clitoris, mucous membrane of glands, &c.

COMPOUND TACTILE SENSATIONS.

These may be simultaneous or successive.

Simultaneous Tactile Sensations.—Simultaneous sensations may be either double or multiple.

Double Sensations, whether of contact, pressure, or traction, are shown only when the stimuli are applied at a certain distance from one another. If they are near enough, the sensation remains single, although the stimulus has been applied in two places. The earliest systematic experiments on this subject were by H. Weber, who touched the various parts of the skin with the points of a pair of carpenter's compasses, observing the distance of separation necessary to give the sensation of two points of contact. The instrument which is now used for the same purpose is the *æsthesiometer*. The following table from Weber gives the minimum separation necessary for the sensation of double contact:—

Tip of the tongue	..	..	..	1.1 mm.
Palmar surface of ungual phalanx of finger	..	..	..	2.2 "
Red border of lips	..	..	..	4.5 "
Palmar surface of second phalanx	..	..	..	4.5 "
Palmar surface of third phalanx	..	..	..	6.7 "
Tip of nose	..	..	..	6.7 "
Palmar surface of head of metacarpal bones	..	..	..	6.7 "
Median line of dorsum and margins of tongue, to a distance of 2 mm. from the tip	..	..	..	9.0 "

Cutaneous margin of lips	..	..	9.0 mm.
Over metacarpal bone of thumb	..	..	9.0 "
Plantar surface of second phalanx of great toe	..	..	11.2 "
Dorsum of second phalanx of fingers	..	..	11.2 "
Cheek	..	..	11.2 "
Eyelids	..	..	11.2 "
Palatine arch	..	..	13.5 "
Anterior part of malar bone	..	..	15.7 "
Plantar surface of metatarsal of great toe	..	..	15.7 "
Dorsal surface of first phalanx of fingers	..	..	15.7 "
Dorsal surface of head of metacarpal bone	..	..	18.0 "
Internal surface of lips	..	..	20.3 "
Posterior part of malar bone	..	..	22.5 "
Lower part of forehead	..	..	20.2 "
Back of heel	..	..	22.5 "
Lower part of occipital region	..	..	27.0 "
Back of hand	..	..	31.5 "
Neck, beneath the chin	..	..	33.7 "
Vertex	..	..	33.7 "
Knee	..	..	36.0 "
Sacrum	..	..	40.5 "
Buttocks	..	..	40.5 "
Fore-arm	..	..	40.5 "
Leg	..	..	40.5 "
Dorsum of foot	..	..	40.5 "
Sternum	..	..	45.4 "
Neck	..	..	54.1 "
Back	..	..	54.1 "
Thigh, arm	..	..	67.6 "

This proceeding measures, with tolerable accuracy, the degree of sensibility of the various regions of the skin. We thus find that it increases from the central end of a limb towards its periphery. It varies with the extent of movement, being, for each segment of a limb, proportional to the distance of the points of the skin from the axis of rotation of the limb. It increases slowly as we pass down the arm and fore-arm, more quickly in the hand, and still more so in the fingers. On account of this change of sensibility, the points of the compass seem to diverge, if the points are moved down the limb, while the same separation is preserved, and *vice versa*.

The minimum separation is less in the horizontal direction than in the vertical; it is less in infancy than in adult life; it diminishes by attention and by exercise (as seen in the blind); it is also diminished when the skin is moistened with an indifferent fluid (water or oil); it increases when the skin is stretched (as seen in pregnancy).

Electrisation of the skin between the points of the compass, or drawing a line with the point of a pencil (or such instrument) from one to the other, causes the double sensation to disappear.

Multiple sensations.—If a compass with several branches be used, it is found that by increasing the number of points, the sensation loses its distinctness; beyond four or five points confusion follows, and it becomes impossible to define the number.

Successive tactile sensations.—If tactile sensations succeed too rapidly, they cause a continuous sensation. If the fingers be brought into contact with the teeth of a revolving wheel in motion, the impressions are fused when the number of shocks felt amount to 640 per second, and the teeth of the wheel can no longer be distinguished.

Under certain conditions successive tactile sensations cause a special compound sensation of peculiar character, such as we experience in *itching*.

Characters of tactile sensations.—The *duration* of tactile sensations is somewhat longer than that of the application of the stimulant, the wheel experiment above-mentioned shows that the consecutive sensation for each shock of a tooth of the wheel lasts $\frac{1}{8}$ of a second.

An important character of tactile sensations is its *exteriority*. Tactile sensation is always referred to the limit of the cutaneous surface, and in some cases it is referred to the exterior. For instance, if we touch the ground with the end of a cane, we feel the ground; if the cane is held loosely in the hand we have two sensations, that of the cane at the surface of the skin, and that of the ground externally. This tendency to refer all tactile sensations to the surface explains the *projection* of painful sensations which is experienced when sensory nerves are irritated in their course, and in case of amputated limbs.

Another essential character of tactile sensations is their *localisation*. This enables us to know, more or less exactly, the point on the surface which has been touched or pressed. This power of localisation is probably the resultant of a series of psychical acts; and the connection between the mental and physical conditions explains certain illusions of tactile sensation, of which the best known is the so-called experiment of Aristotle, represented in fig. 50. When a small ball is rolled between the crossed index and middle finger, there is a sensation

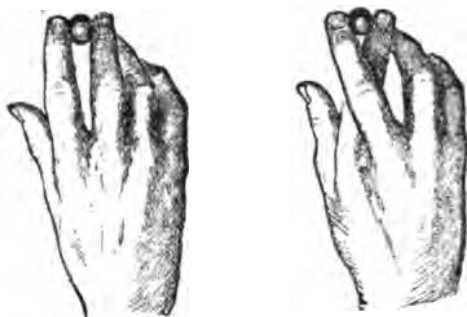


Fig. 50.

of two balls being present, instead of one, as when in the position represented on left figure.

Causes which influence tactile sensations.—The causes which influence tactile sensibility are referable—some to the skin, and some to the state of the body brought into contact with it. The presence of the epidermis is indispensable, but its thickness and hardness diminish tactile sensation. The same result is produced by hyperæmia or anæmia of the skin, or by lowering its temperature (as in the local anæsthesia produced by the ether spray). The presence of hairs or down increases the sensibility to pressure, so the sensation of contact is less in shaven parts. Feeble induction currents diminish sensibility; the use of baths of water saturated with carbonic acid increases it.

The *temperature* of the touching body also influences it; a given weight appears heavier than an equal weight when warmer; the two points of the compass are more distinctly felt when their temperature is unequal, &c. As already mentioned, it is modified by exercise, and attention, which gradually increase it; and a very remarkable fact is that the exercise of the tactile sensibility of the part, increases that of the corresponding part of the opposite side of the body. Exercise also increases the sensibility to pressure. This is estimated by placing different weights successively on the same part of the surface, and judging the difference without using the eyes. According to Weber, a difference of $\frac{1}{40}$ is distinguished, when the body is not too light or too heavy.

The sensation of contact is diminished by *habitude* (*i.e.*, when the contact is continuous). This is exemplified by the fact, that we do not perceive the contact of our garments, which we are always wearing. The influence of fatigue has not been studied with care up to the present.

Tactile sensations sometimes produce reflex actions; varying according to the surface engaged, and mode of stimulation employed. Examples of this effect are seen in the laughing and convulsive movements produced by tickling, the coughing produced by titillation of the external auditory meatus, and the sneezing caused by irritation of the nasal mucous membrane.

SENSATIONS OF TEMPERATURE.

The sensation of temperature requires for its production a *sudden* change in the temperature of the skin. The latter is maintained by the temperature of the blood, and, except in rare cases, is somewhat higher than that of the surrounding atmosphere, and lower than that of the deep parts of the body, so that, under ordinary circumstances, the skin undergoes (1) a continual loss of heat to the surrounding medium, and (2) a continual gain from the deeper parts. When these conditions are equably maintained, there is no sensation of temperature felt; that of the surface remains constant and uniform.

It is obvious, from what we have already said, that the sensation of cold may be produced by one of two causes: (*a*) diminution of the heat conveyed from the interior, as in case of contraction of the cutaneous arteries; (*b*) an increase of the loss of heat from the surface, as by contact with a colder or better conducting surface than the one previously in contact with the skin. The sensation of heat is produced under the opposite circumstances: (*a*) when there is an increase of the heat from within, as produced by dilation of the superficial vessels; or (*b*) if the loss of heat from the surface is less rapid than the gain from within.

All bodies, whatever be their state, solid, liquid, or gaseous, are able to produce sensations of loss of temperature; there are only two things to be considered: the temperature of the touching body, and its conductivity. If the temperature be very high or very low, the sensation of temperature is lost in that of pain. At equal temperatures, the better conducting

bodies (e.g. metals) produce more intense sensations of heat or cold. This is markedly exemplified in the difference of contact with air and water. If, when the air is at 17°C ., the hand is plunged into water at 18° , there is a sensation of cold produced, which is accounted for by the fact that as water is a better conductor, the hand loses heat more rapidly in that fluid. For the same reason a piece of metal always feels warmer (or colder) than a piece of wood at the same temperature.

CHARACTERS OF SENSATIONS OF TEMPERATURE.

As the temperature of a body which touches the skin varies, it produces one of two sensations—that of heat, or that of cold. These are fundamentally but differences of degree, but the sensations experienced are widely different. When these sensations reach a high degree of intensity pain is felt, which at first has special characters for heat and cold, but, when it reaches the maximum, takes on in both cases the character of burning.

To estimate the thermic sensibility of the skin a compass has been employed, of which the points have been unequally heated: the *asthesiometer of Liegeois*. It is constructed on the same principles as the ordinary instrument, but the points are connected with small hollow prisms, which contain fluids of different temperatures.

The thermic sensibility of the different regions of the skin does not correspond exactly to the localisation of the tactile sensibility. It is best marked on the cheeks, eyelids, tip of tongue, and external auditory meatus; it is much less on the lips, and very feeble on the nose. On the trunk, the sensibility diminishes as we approach the median line; the sensibility of the surface diminishes from below upwards; the abdomen is more sensitive to change of temperature than the back; on the limbs the sensibility increases as we approach the trunk; in the arm and thigh the extension aspect is more sensitive than that of flexion; the reverse is the case in the fore-arm and leg. It is diminished by cold, by heat, and by increased thickness of the epidermis.

The *intensity* of the sensations produced by temperature depends on the temperature and conducting power of the body

touched ; and, in addition to this, it is modified by the extent of surface engaged : for instance, water appears hotter or colder when the whole hand is submerged than if only a finger has been dipped in.

The *duration* of the sensation is longer than the application of the stimulant. On this account there are *consecutive* sensations of heat or cold remaining, which also possess the peculiarity of not subsiding uniformly, but undergoing elevations during the fall.

The *localisation* of thermic sensations, although always correctly referred to the part touched, is more diffuse, and much less sharply defined than that of tactile sensibility.

The thermic sensibility of mucous membrane is, as a rule, much less than that of the skin. It is pretty well developed in the buccal and pharyngeal mucous membrane (the velum pendulum palati distinguishes a difference of 2° C.), but the mucous membrane of the stomach and intestinal canal, uterus, &c., possess none.

INTERNAL SENSATIONS.

The internal sensations are distinguished from the others described by their vague character, and the difficulty of localising them in any special situation. But their most distinctive character is the fact that they only inform us about the general state of the organism without ever putting us in relation with external objects.

These internal sensations are probably very complex ; the exercise of each function is accompanied by certain sensations, which usually pass unperceived on account of their feebleness and the continual habit of bearing them. They, under certain conditions, acquire a high degree of intensity, and may even become intolerable. Of these internal sensations there are two varieties : one class corresponds to the non-exercise of function, and the other to its exercise.

(1.) The first class is that to which the French writers give the name of *besoins* ; the English language has no good word to express it. If the respiratory movements be checked for some time, the well-known sensation of intense distress in the chest makes the condition unbearable ; hunger, thirst, the desire to sleep, &c., are all sensations of the same order. When such

sensations are of very slight intensity, they have sometimes an agreeable character ; such as appetite for food, sexual desire, &c. ; but when they attain a certain degree of intensity, they always become disagreeable. Some are always disagreeable, such as nausea.

(2.) The second class of internal sensations correspond to the exercise of the physiological functions of the system. Of this we have a good example in the sense of *bien-être* which accompanies the inspiratory act, after the breath has been held for a long time. The same sensation of euphoria is experienced when the calls of hunger or thirst are satisfied, or even during muscular exercise ; and these pleasurable sensations sometimes attain a high degree of intensity, as during sexual congress. They are called by some writers *internal functional sensations*.

(3.) *Pain*. The sensation of pain is but an exaggeration of the normal sensation, and appears when the latter reaches too great a degree of intensity.

The sensation of pain is specially acute in these organs which are endowed with tactile sensibility, but is experienced in parts where no sensation exists in the normal state, and it may be broadly asserted that all parts supplied with nerves may become the seat of painful sensations.

With regard to the production of pain, the organs may behave in one of two ways. Some are painful when irritated from without (by pricking, section, &c.) ; other structures, on the contrary, may be pricked, cut, or torn without eliciting any pain. They are ordinarily spoken of as insensible, yet they suffer severe pain from internal causes, such as cramp, fatigue, &c.

The *character* of pain varies extremely, according to the tissues engaged, and the nature of the irritant ; these are expressed by different terms which express their nature more or less accurately, such as acute, pungent, boring, gnawing, lancing, terebrating, &c.

The *localisation* of painful sensations is usually very indistinct, and vaguely diffused, but in some instances we find it limited to a very narrow area, or traceable along the course of the nerve or nerves engaged.

The *intensity* of pain depends on the intensity of the irritation and duration of its application, on the irritability of the

individual and on that of the part affected, as well as on the copiousness of the nervous supply of the latter.

Whether special nerve-fibres are set apart for the conveyance of painful sensations has not been proved, although asserted by some observers.

PHYSIOLOGY OF THE NERVES.

Roots of the Spinal Nerves.—(1.) *Anterior roots.*—The functions of the roots of the spinal nerves were first demonstrated by Sir Charles Bell. The anterior roots are motor: this is shown by section, after which the corresponding areas of innervation are found to have lost all their movements; stimulation of the central end has no effect, while stimulation of the peripheral end causes active contractions. According to some authorities (Steinmann, Cyon, &c.), the irritability of the anterior roots is influenced by the posterior; the latter convey the stimuli by which the muscular tonicity is maintained, so that after their section the height of the contraction is diminished. These results have, however, been contradicted by many other observers.

The anterior roots also contain other special fibres: vasomotor, secretory, trophic, &c.

Posterior roots.—The posterior roots of the spinal nerves are *sensory* (sensitive to pain, tactile sensations, &c.). After section of these roots the parts supplied by the corresponding nerves are no longer sensible to pain: pricking, burning, electricity, &c., of the peripheral extremity causes no result, while if the central end be irritated, signs of pain follow. We also find that section of the posterior roots does not affect the power of motion in the parts.

The irritability of the posterior roots disappears very soon after death, while that of the anterior roots persists a considerable time.

Recurrent sensibility.—Magendie and Cl. Bernard have described under this name (*sensibilité récurrente*) the sensibility of the anterior roots which is due to the recurrent fibres coming from the ganglia or posterior roots, and passing into the anterior roots at the peripheral end. This sensibility disappears after section of the posterior roots; while, if the anterior roots alone are divided, the peripheral segment retains its sensibility, but

the central portion is found to have lost it. The place where the sensory fibres turn back to join the anterior has not yet been determined. According to Cl. Bernard the communication is peripheral, for section of the mixed nerves, which proceed from the junction of the roots, is followed by complete abolition of the recurrent sensibility, and the results of the experiments of Arloing and Tripier are still more conclusive.

Spinal Nerves.

These contain : (1) fibres from the anterior roots ; (2) fibres from the posterior roots ; (3) fibres from the sympathetic ; and, accordingly, they combine the physiological properties of all three kinds of nerves. The nerve trunks are usually divided into sensory, motor, and mixed, from the preponderance of the fibres, which make up the greater part of their bulk. But, in addition to these nerve-fibres, vaso-motor filaments also travel with them, and probably several other kinds of fibres.

Cranial Nerves.

Ten cranial nerves were enumerated by Willis, who included the sub-occipital, and included as a single nerve all the trunks that passed out through a single foramen. Sömmerring, who classed the sub-occipital with the spinal nerves, and enumerated the other nerve-trunks singly, increased the number of cranial nerves to twelve.

(1.) **First cranial nerve** (*nervus olfactorius*).—This is the nerve of smell. After section of its trunk on both sides, the sense of smell is completely lost ; but the mucous membrane is still sensible to tactile stimulants, such as ammonia. It was asserted long ago by Diemerbroeck and Mery, and subsequently by Magendie, that the sense of smell remained after destruction of the olfactory nerves, but this is certainly not the case ; and their results have been contradicted by nearly all physiologists. In the remarkable case of congenital absence which was found by Cl. Bernard (case of Maria Lemens), there was a probable history of some olfactory sensibility having existed during life ; but the evidence, although it seems to have somewhat shaken the faith of Bernard himself with regard to the absolute dependence of the sense of smell on these nerves, is not enough to invalidate the universal experience of a host of other enquirers.

(2.) **Second cranial nerve** (*nervus opticus*).—The researches of recent histologists, especially of Axel Key and Retzius, have shown that this nerve possesses three distinct sheaths formed by prolongations of the membranes of the brain itself: (a) an external derived from the dura mater (*dural sheath* of Axel Key and Retzius); (b) a middle derived from the arachnoid (*arachnoidal sheath* of Axel Key and Retzius); and (c) a connective-tissue sheath derived from the pia mater. Between the dura-matral and arachnoidal sheaths is the *subdural lymph space* of Axel Key and Retzius (*subvaginal space* of Schwabe), which communicates with the subdural space within the cranium; and between the arachnoidal and pia-matral sheaths is another lymph-space, the *sub-arachnoidal space* of the optic nerve (Axel Key and Retzius), which, however, does not communicate with the sub-dural. A large *sub-pial* lymph-space also exists, which is separate from the sub-arachnoid, but communicates freely with the endoneural spaces between and around the nerve-fibres.

The pial sheath form the *perineurium*, the whole nerve being comparable to a compound nerve-bundle (Klein), and the component fasciculi have not special perineural sheaths, as in case of the spinal nerves, the investing sheaths being all continuous with the pia mater.

The fibres are medullated nerve-fibres, which do not possess a sheath of Schwann, and the interstitial substance is identical in structure with neuroglia.

Most of the fibres decussate at the chiasma, but some of the outer ones pass on to the eye of the same side (some authorities, however, assert that the decussation is complete). Some of the fibres turn back to the opposite side of the brain (*inter-cerebral*), and some pass between the retinæ of opposite sides (*inter-retinal fibres* of Mayne). The accompanying illustration shows the probable arrangement of the fibres of the optic tracts, and explains the result of lesions of the chiasma, optic tracts, and tubercula quadrigemina from which they take origin.

This is the nerve of vision; section produces blindness (*amaurosis*); stimulation produces luminous sensations; if light is brought to fall on the fibres, no result is produced; luminous sensations are only produced by the intervention of the retina.

Third cranial nerve (*nervus motor oculi communis*).—This is a purely motor nerve. It supplies, by its upper branch,

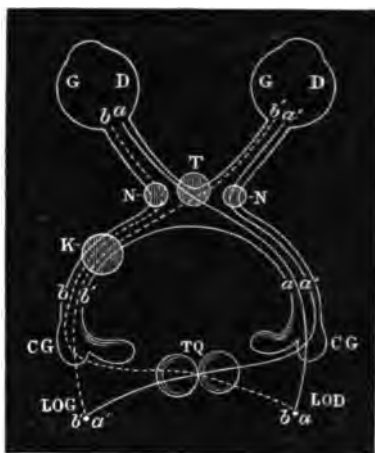


Fig. 51.

Diagram of Optic Nerve Fibres (Charcot). CG, corpora geniculata. b'a, *decussating*; a'b, *non-decussating* fibres. TQ, shows crossing of the latter, behind the corpora geniculata (CG); K, lesion producing right lateral hemiopia; LOG, lesion producing right amblyopia; T, NN, lesions producing temporal and nasal hemiopia.

the *levator palpebræ superioris*, and *rectus oculi superior*; by its inferior branch, the *rectus internus*, *rectus inferior* and *obliquus inferior*. The branch which supplies the latter muscle sends the motor root to the ciliary ganglion, and by means of this twig supplies the *sphincter pupillæ* and the *tensor choroidæ* (Bowman's *ciliary muscle*). Accordingly, it has the following actions on the eye-ball and its appendages:—(1) It elevates the upper lid, and on this account permanent dropping of the lid (*ptosis*) follows paralysis of this nerve. (2) It presides over the upward, downward, and inward rotation of the eye-ball, and the rotation on its antero-posterior axis, caused by the action of the *obliquus minor*. Accordingly, after its paralysis, the eye-ball is rotated downwards and outwards by the combined action of the external rectus and the superior oblique; there is crossed diplopia, and the images are seen only in a limited portion of the field of vision. The image on the paralysed side is a little higher than that on the sound side, and at its upper end inclines towards the median line. The rotation of the eye-ball on its antero-posterior axis is limited, and cannot be effected when

the eyes are directed upwards and outwards. (3) On account of its supplying the sphincter pupillæ, permanent dilation of the pupil (*mydriasis*) follows section or paralysis of this nerve, while intra-cranial galvanisation produces close contraction (*myosis*). The pupil, however, dilates still further under the influence of atropin than by galvanisation of the sympathetic, and a very slight contraction follows, in some cases, section of the sympathetic nerve, or of the ophthalmic. (4) The influence of this nerve on accommodation has not been finally settled even yet. The fibres which preside over accommodation seem to be intimately connected with the branch which supplies the levator palpebræ superioris; for, in those cases of partial paralysis, where the latter muscle is not affected, accommodation remains intact. In some cases of paralysis of the motor oculi, accommodation has remained, but it was observed that in these cases the movements of the iris were not abolished, so that some fibres probably remained unaffected. Stimulation of the trunk of the nerve is followed by variation in the reflected image formed on the anterior surface of the crystalline lens, similar to what is seen in accommodation (Trautvetter), and direct stimulation of the ciliary nerves causes increased convexity of the anterior surface of the lens (Hensen and Vœlckers). The influence of this nerve on accommodation explains the contraction of the pupil which exists when we examine near objects, and the dilation which follows when the attention is directed to objects at a distance; we are able in this way to cause contraction or dilation of the pupil at will. (5) The tonic contraction of the recti muscles opposes the pressure of the retro-bulbar tissues, and on this account a slight degree of exophthalmos is observed to follow section of the motor oculi nerve.

Sensibility.—According to Valentin and Adamük the motor oculi contains sensory fibres from its origin, and evidences of pain follow irritation of its trunk within the cranium. According to most other authorities who have investigated the subject (Longet, Arnold, &c.), it contains no sensory fibres at its origin, and the sensibility which it possesses further on is due to its anastomosis with the ophthalmic. Claude Bernard found in the intra-cranial portion of the nerve evidences of *recurrent sensibility* due to the ophthalmic.

Anastomoses.—(1) With the *ophthalmic*. This communica-

tion is generally admitted to be the source of sensibility of the motor oculi nerve; but its existence is denied by Arnold and Bischoff. (2) With the *carotid plexus*. This probably gives the vaso-motor filaments to the muscles. (3) With the *sixth* nerve. This communication probably does not exist, although admitted by some authors.

Fourth cranial nerve (*nervus patheticus; n. trochlear*; Sir Charles Bell's *respiratory nerve of the eye*). This nerve supplies a single muscle (the *obliquus oculi superior*), and in this way presides over the movement of the eye-ball by which the pupil is directed downwards and outwards.

Fifth cranial nerve (*trigeminus* vel. *trifacialis*). This is a mixed nerve, containing motor, sensory, and perhaps special sense fibres. It was called by Sir Charles Bell the *spinal nerve of the head*, on account of the striking resemblance between it and a spinal nerve, as it has two roots, of which the anterior is small and motor, while the posterior is large, sensory, and furnished with a ganglion.

Motor root.—The distribution of the motor part of this nerve is to the muscles of mastication. It supplies the temporal, masseter, both pterygoids, the mylo-hyoid, and anterior belly of digastric. It also supplies the tensor palati, according to some authorities; Hein has seen contractions in the soft palate produced by stimulation of the motor root, but against this idea we have the fact that this muscle usually escapes in paralysis of the nerve. The buccal nerve was formerly believed to be motor, but it merely pierces the buccinator muscle, which it was supposed to supply with some of its motor fibres. This muscle is wholly supplied by the facial nerve.

(1) **OPHTHALMIC NERVE of Willis.**—The functions of this nerve are complex, and may be considered in the following order:—

Sensory function.—This branch furnishes sensory fibres (1) to the skin of the corresponding side of the forehead, upper eye-lid, and side of nose; (2) to the conjunctiva, mucous membrane of the lachrymal passages, frontal sinuses, and anterior part of the nasal fossæ; (3) to the cornea, iris, sclerotic, and choroid; (4) to the periosteum of the frontal and orbital regions, and anterior part of the nasal cavity. It probably furnishes muscular sensibility to the muscles of the orbit (Sappey), and perhaps to the muscles of the frontal region and the sphincter oculi.

Secretory function.—The secretion of the lachrymal gland is under the influence of this nerve; this is shown by the result of irritation of the peripheral segment of the nerve, which produces a copious secretion of tears; its section first stops the secretion, but, after some time, a continuous flow of tears (probably paralytic) appears. Stimulation of the ophthalmic also produces a flow of tears, which stops when the lachrymal branch is divided.

Trophic function.—After section of the ophthalmic nerve, the nutrition of the eye-ball is found to be specially affected. The changes (which were first studied by Magendie) usually commence in the cornea, which becomes turbid and vascular, and soon becomes the seat of an ulcerative keratitis, which may lead to perforation; the conjunctiva and iris also become reddened and inflamed. Diminution of the intra-ocular tension accompanies these changes (Kocher), while an increase of the tension of the eye-ball has been seen to follow stimulation of the trifacial nerve (Hippel and Grünhagen).

According to some authorities, however, these changes are merely due to mechanical irritation of the foreign bodies, of the presence of which the animal has no consciousness; they have also been attributed to the drying of the conjunctiva, from diminution of the lachrymal secretion, and absence of winking movements. It was observed by Magendie that section of the nerve after leaving the Casserian ganglion affected nutrition much more than section of the nerve-trunk, before crossing the petrous portion of the temporal bone. The changes were referred by Magendie to section of the sympathetic fibres which accompany the nerve, as corresponding trophic changes have been observed to follow removal of the superior cervical ganglion. Claude Bernard has, however, shown that there is an antagonism between the action of the trifacial and the sympathetic; section of the former causing a lowering of temperature of the corresponding side of the face, and removal of the superior cervical ganglion appearing to check the ocular lesions which supervene upon section of the trifacial.

Schiff and V. Bezold attributed the changes to paralytic dilation of the blood-vessels from section of the vaso-constrictor fibres coming from the medulla oblongata; while the experiments of Claude Bernard go to prove that they are really due to section of the vaso-dilator fibres which come from the brain and the Casserian ganglion. The destructive changes occur without degeneration of the nerve fibres, which is against the idea that they are due to lesion of the trophic nerves.

Action on the iris and pupil.—The ophthalmic nerve contains all the dilator fibres of the pupil. We shall consider these with the structure and functions of the iris.

Vaso-motor action.—The ophthalmic nerve contains vaso-motor

fibres for the iris, choroid, and retina. They probably come from the communicating branches of the sympathetic, although some authorities (Klein, Svetlin) assert that no change of the retinal vessels follows either stimulation or section of the sympathetic.

Ciliary ganglion.—Removal of this ganglion is followed by immediate insensibility of the cornea, but the ganglion itself has been found insensible by Claude Bernard; its ciliary branches are sensitive, and contain (as we shall see later on) some constricting and some dilating fibres of the pupil.

The short root of the ganglion probably furnishes branches to the sphincter iridis; the long root gives sensory branches to the iris and cornea, while the sympathetic root probably furnishes vaso-motor filaments to the blood-vessels.

Anastomoses.—The communications of this nerve with the third, fourth (?), and sixth probably supply muscular sensibility to the muscles supplied by these nerves. The communication with the carotid plexus contains some of the vaso-motor fibres of the ophthalmic.

(II) SUPERIOR MAXILLARY NERVE. *Sensory action.*—This nerve supplies sensory fibres to (1) skin of lower eye-lid, cheek, ala nasi, and upper lip; (2) to the mucous membrane of the nasal, palatine, and pharyngeal regions, also to the sinus maxillaris, upper lip, gums, and Eustachian tube; (3) to the dura-mater, periosteum, and bones, which correspond to its distribution; (4) to the teeth of the upper jaw; (5) to some of the facial muscles.

Secretory action.—It furnishes branches to the nasal, palatine, and other mucous glands along the area of its distribution; its temporo-malar branch sends a twig to the lachrymal gland, and stimulation of the nerve is followed by a flow of tears (Herzenstein, Voelckers).

Vaso-motor action.—This nerve sends vaso-motor fibres with the arteries of the nasal fossæ, but they are probably derived from the sympathetic.

Trophic action.—Section of the trifacial has been followed by changes in the nasal mucous membrane, which becomes vascular, with increased secretion of mucus, and the nutritive disturbance even goes on to the formation of fungous ulcers.

Influence on the olfactory function.—This nerve influences the sense of smell in two ways: (1) by its vaso-motor fibres it

influences the healthy nutrition of the mucous membrane ; (2) by its secretory fibres it presides over the moisture of the parts, which is essential for the exercise of this sense.

Excito-reflex action.—Stimulation (especially mechanical) of the palatine branches produces reflex movements of deglutition, which disappear after section of the trifacial nerve (Prevost and Waller). Stimulation of the cutaneous filaments, and more especially of the nasal branches, causes a reflex secretion of tears.

Spheno-palatine ganglion.—Extirpation of this ganglion is not followed by change of vascularity or sensibility in the nasal mucous membrane, nor by any alteration of taste or smell. Stimulation of the ganglion is followed by a flow of nasal mucus on the same side, accompanied by an increase of temperature.

The motor and sympathetic roots come through the Vidian nerve, from the facial nerve and carotid plexus respectively. The sensory root comes from the superior maxillary. The motor branches are distributed to the levator palati and azygos uvulæ. The sensory branches supply the nasal and palatine mucous membranes. The naso-palatine nerve was found by Claude Bernard to be void of sensibility ; it takes origin from the nerve-cells of the ganglion. The spheno-palatine branches of superior maxillary pass through the ganglion, and form the palatine nerves.

Anastomoses.—These are the communications with the facial and the carotid plexus already mentioned.

(III) INFERIOR MAXILLARY NERVE. *Sensory action.*—This nerve furnishes sensory branches : (1) to the skin of the cheeks, the lower lip, chin, part of auricle, and external auditory meatus ; (2) to the mucous membrane of the cheeks, lips, gums, anterior part of tongue, part of the tympanum and mastoid cells ; (3) to the dura-mater, lower jaw, temporal bone, and the periosteum ; (4) to the temporo-maxillary articulation ; (5) to the corresponding muscles (muscular sensibility).

Gustatory functions.—According to most authorities, the gustatory nerve presides over the special sense of taste in the anterior two-thirds of the tongue. Section of the nerve has been found in man to be followed by loss of taste in this region, especially for saccharine substances. Many,

however, believe that these fibres come from the chorda tympani nerve.

Auditory function.—Lesions of this nerve indirectly impair the sense of hearing, through the muscular, sensory, and glandular branches, which it distributes to the organs of hearing.

Secretory function.—This nerve presides over the secretion of the glands of the buccal mucous membrane; and, according to Remak, small microscopic ganglia are placed on the fibres close to their terminations. Its influence on the salivary secretion we shall see later on.

Trophic function.—This has not been determined with sufficient accuracy up to the present.

Reflex function.—Stimulation of the lingual produces a reflex secretion of saliva. The movements of suction in the infant are also due to reflex irritation of the inferior maxillary nerve.

Motor function.—The small root of the trifacial nerve (*n. facialis profundus* of Fäsebeck) supplies the muscles of mastication, already mentioned.

Otic ganglion.—Arnold has described the roots of this ganglion: a motor root from the inferior maxillary nerve, which, according to Hyrtl, comes from the nerve to the internal pterygoid muscle, when it touches the ganglion. Longuet, however, derives the motor root from the facial, through the small superficial petrosal; but this idea is disproved by the fact that the tensor palati and tensor tympani muscles, which receive their nerves from the ganglion, are paralysed by section of the fifth nerve. The sensory root is a branch of the glosso-pharyngeal, from the tympanic nerve of Jacobson, passing with the lesser and external petrosal nerves; according to Hyrtl and Rüdinger, it comes from the inferior maxillary nerve. The sympathetic root comes from the plexus on the middle meningeal artery. The ganglion also receives parotidean branches from the lesser superficial petrosal.

Its branches are distributed: (1) sensitive twigs, to anastomose with the auriculo-temporal, or lesser superficial petrosal, from which they pass to the mucous membrane of the tympanum; (2) parotidean branches (originally from the facial), which join the auriculo-temporal; (3) motor filaments, to the tensor palati and tensor tympani; (4) an anastomotic twig to the chorda tympani, whose use is unknown.

Submaxillary ganglion.—This ganglion, from analogy to the

others, has been furnished by anatomists with three roots, a motor from the chorda tympani, a sensory from the gustatory branch of inferior maxillary, and a sympathetic from the plexus on the facial artery.

(1) The chorda tympani sends twigs to the ganglion (originally from the facial). Through this the facial presides over the secretion of the submaxillary gland, as it does over that of the parotid and sublingual. Intra-cranial stimulation of the facial nerve produces a flow of submaxillary saliva (Ludwig). Stimulation of the chorda tympani causes a copious secretion, which has also peculiar characters (Bernard's *chorda saliva*). Stimulation of the chorda tympani causes dilation of the vessels of the gland.

(2) Stimulation of the sympathetic branches which come to the ganglion from around the facial artery causes salivary secretion, but the fluid produced (Bernard's *sympathetic saliva*) differs from the chorda saliva in important particulars, as we shall see later on. The sympathetic root also contains vaso-constrictor fibres, the stimulation of which causes constriction of the blood-vessels of the submaxillary gland.

(3) According to Bidder, the sensory root from the gustatory nerve consists of two parts: (a) central, from the central segment of the chorda tympani nerve, and (b) a peripheral root, from the distal segment of the nerve, which does not degenerate after section of the chorda tympani.

The question whether the submaxillary ganglion can act as a reflex centre has not been conclusively settled up to the present. We shall consider it when we come to examine the physiology of the saliva.

Sixth cranial nerve.—This is, at least at its origin, a purely motor nerve. Cl. Bernard has attributed to it a recurrent sensibility which most other observers have failed to verify. Paralysis causes convergent strabismus, accompanied by diplopia, with double homogeneous images.

Seventh cranial nerve.—This nerve consists of three portions: (1) *Facial (nervus facialis superficialis* of Fäsebeck.) *Motor functions.*—This nerve supplies: (1) the *muscles of expression* of the face; (2) in the neck, it supplies the *stylohyoid* and posterior belly of *digastric*; (3) in the tongue, it supplies, according to Sappey and Hirschfeld, the *stylo-glossus* and *palato-glossus*; (4) of the palatine muscles, it supplies the

levator palati and *azygos uvulae*, by means of the great superficial petrosal nerve (through Meckel's ganglion, and its posterior palatine branch). According to Longet it supplies *all* the muscles of the soft palate, except the tensor, but this description has not been confirmed; the palato-pharyngeus is, chiefly at least, supplied from another source, and probably the palato-glossus.

Sensory function.—The facial nerve is insensible at its origin (Magen die, Cl. Bernard, &c.), and no loss of sensibility accompanies its paralysis. Some authors (Wrisberg, Bischoff, &c.), arguing chiefly from the presence of the *ganglion geniculatum*, look upon the *portio intermedia* as its sensory root, but the latter has been shown by Cl. Bernard to be insensible. However, the facial nerve is undoubtedly sensory after its emergence from the stylo-mastoid foramen. The sensory fibres come from two sources: (a) from the trifacial (along the great superficial petrosal nerve), and (b) from the pneumogastric (through Arnold's nerve).

Gustatory function.—The extent of this function of the *chorda tympani* branch has not been definitely settled. The intra-tympanic section of the nerve has been found by Prevost to be followed by only partial loss of taste in the anterior part of the tongue, while others have found complete ageusia in this region. Bigelow traces the *chorda tympani* nerve as a continuation of the nerve of Wrisberg. Faradisation of the *chorda tympani* was found by Duchenne to be followed merely by salivation and a sensation of tingling in the anterior part of the tongue, but not by a true gustatory feeling.

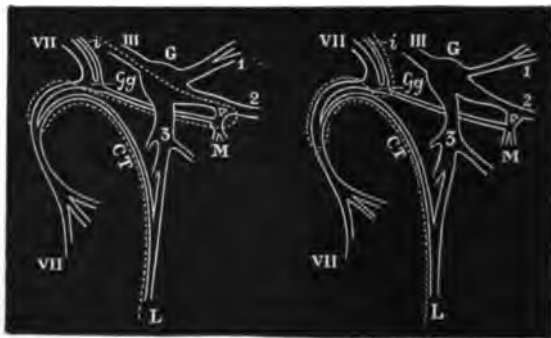


Fig. 51.

Fig. 52.

The theory of Schiff, which is represented in Fig. 51, can hardly be maintained in presence of the fact, demonstrated many years ago by Alcock, that extirpation of the sphenopalatine ganglion causes no diminution of the sense of taste. That of Lussana (Fig. 52) is the same as the view advocated by Bigelow, mentioned above.

Secretory function.—The influence on the salivary secretion shall be studied later on.

Vaso-motor function.—Cl. Bernard has found intra-cranial section of this nerve to be followed by lowering of temperature, while section within the aqueduct of Fallopius was succeeded by an elevation.

Trophic function.—In growing animals, removal of a piece of the facial nerve has been followed by atrophy of the muscles and even bones on that side of the face (Brown-Sequard, Schauta). Loss of hair, changes in the cuticle, and even dry gangrene of the ear, have been observed by Beaunis to follow the same lesion.

(11) *Geniculate ganglion and nerve of Wrisberg.*—As already mentioned, Wrisberg, and others since his time, have looked upon this nerve as a sensory root of the facial. Longet describes it as the motor nerve of the tympanum (*nerf moteur tympanique*); supplying the *stapedius* and *tensor tympani*. Cl. Bernard looks upon it as part of the sympathetic, sending its fibres to the petrosal and chorda tympani nerves, which preside over the mucous and salivary secretions. Lussana and Bigelow regard it as gustatory in function.

Anastomoses.—(1) A communication exists in the internal meatus between the facial and auditory nerves. Its use is unknown. (2) By means of the great superficial petrosal, with Meckel's ganglion, to supply the muscles already named. (3) Through the lesser superficial petrosal and otic ganglion it sends filaments to the auriculo-temporal nerve and parotid gland. (4) With the auricular branch of the pneumogastric (Arnold's nerve). (6) With the glosso-pharyngeal.

(111) *Auditory nerve.*—The functions of this nerve will be more profitably studied with those of the organ of hearing itself.

Eighth cranial nerve.—This nerve consists of three portions: (1) GLOSSO-PHARYNGEAL NERVE. *Sensory action.* This nerve is sensitive from its origin, and it furnishes sensibility to the

mucous membrane of the posterior segment of the tongue, pillars of fauces, tonsils, and anterior surface of epiglottis. Through its pharyngeal branches it probably aids in the sensory supply of the pharyngeal mucous membrane. It also (with the trifacial) supplies the mucous membrane of the tympanum, mastoid cells, and Eustachian tube.

Reflex function.—Irritation of part of the mucous surface supplied by this nerve produces the reflex actions of nausea and vomiting. After division of the glosso-pharyngeal, irritation of the back of the tongue and pillars of the fauces produce no such movements. Movements of deglutition are found to follow stimulation of the central and of the divided nerve. It is also followed by reflex salivary secretion, more copious than that produced by stimulation of the central end of the gustatory.

Gustatory function.—This nerve supplies the special sense of taste to the posterior part of the tongue. Section is followed by abolition of this sense at the region named, especially for bitter substances. Panizza formerly believed that this was the sole nerve of taste, and this opinion has been recently advocated by Carl and by Urbantschitsch. According to Carl, the gustatory fibres take the following course from the brain: glosso-pharyngeal, nerve of Jacobson, lesser superficial petrosal, otic ganglion, trunk of inferior maxillary, and its gustatory branch.

Motor function.—The glosso-pharyngeal sends a branch to the stylo-pharyngeus muscle, but its influence on the other muscles is obscure. Contraction of the upper fibres of the superior constrictor of pharynx, and some of the fibres of the palatine muscles have been seen to follow its stimulation. Some difficulty of deglutition was observed by Magendie to follow section of this nerve; but this result is not usually seen, and is attributed by Longet to section of the pharyngeal branch of the spinal accessory nerve, instead of that of the glosso-pharyngeal.

Secretory function.—This will be described in the chapter on digestion.

Vaso-dilator function.—Stimulation of the peripheral end was found by Vulpian to produce dilatation of the vessels of the base of the tongue.

Anastomoses.—(1) *Nerve of Jacobson.* This branch commu-

nicates with the great superficial petrosal nerve, with the lesser superficial petrosal nerve, and with the carotid plexus. On this nerve, as it breaks up to form the tympanic plexus, ganglionic cells are found.

(2). *With the stylo-hyoid branch of facial.*—This communication conveys most of the motor fibres of the glosso-pharyngeal, particularly the branch to the stylo-pharyngere.

(3). *With the pneumogastric.*—A communication exists between the ganglion of Andersch, and the trunk of the pneumogastric and Arnold's auricular branch. It contains motor fibres from the pneumogastric which go to the palatine muscles, and probably also sensory fibres.

(4). A communication exists between the ganglion of Andersch and the superior cervical ganglion. Its function is not known.

(II). PNEUMOGASTRIC NERVE. *Sensory function.*—The sensibility of the intracranial portion of the nerve has been shown by Claude Bernard. After giving off the very sensitive superior laryngeal branch this property is greatly diminished. The sensory branches are distributed: (1) To the *mucous membrane of the air passages*, from the opening of the glottis to the terminal ramifications of the bronchial tubes. Above the rima glottidis the sensibility is exquisite, but of an entirely peculiar character—the slightest contact of a foreign body produces a violent cough; below the rima, on the other hand, the sensibility has been found by experiment to be extremely obtuse. (2) To the *heart*: if the sinus venosus of the frog be touched with an acid, reflex convulsions of the whole body follow; this result does not follow if the pneumogastric has been previously divided. (3) Is a *part of the digestive tract* of mucous membrane; base of tongue, palate, pharynx, œsophagus, stomach, and probably a part of the small intestine. (4) To the *muscles* to which it is distributed. (5) To the mucous membrane of the *biliary ducts* and *gall bladder*. (6) To the tract of *dura mater* in the region of the *transverse* and *occipital* sinuses. (7) To the posterior part of the meatus auditorius externus.

Besides the above distribution, the vagus is supposed to preside over the sensations of *hunger*, *thirst*, and the *besoin de respirer*. Yet these sensations are not abolished after section of the vagi (Sédillot, Claude Bernard, Longet).

Motor functions.—Stimulation of the vagus at its origin has been found to produce contractions of the *pharyngeal constrictors*, of the *œsophagus*, and of some of the muscles of the *soft palate* (Chauveau, Eckhard, Claude Bernard). Yet Longet asserts that all its motor branches are derived only from its anastomoses with other nerves, especially the spinal accessory.

The motor branches of this nerve supply:—(1) Of the digestive tube: (*a*) some of the palatine muscles (*azygos uvulae*, *levator palati*, and *palato-pharyngeus*): (*b*) the constrictors of the pharynx (according to Chauveau, all the pharyngeal muscles); (*c*) the œsophageal muscular fibres; section of the pneumogastrics abolishes the third stage of deglutition, by paralysing the œsophagus; stimulation of the peripheral end produces not a peristaltic action, but tetanic contraction of the œsophagus along its whole length (Mosso, Ranvier); but even during this contraction, deglutition, once commenced, goes on as in the intact organ (Chauveau, Ranvier). (4) To the stomach: contractions of the stomach follow stimulation of the peripheral segment of the pneumogastric (V. Braam-Houckgeest), but they will not take place if the spinal accessory have been previously divided (Waller). According to Longet, the motor action of the vagus is manifested only when the stomach is full of aliments. According to Chauveau, the motor action of this nerve does not reach beyond the pylorus; but V. Braam-Houckgeest has seen contractions extend into the small intestine.

(2). *Muscle of the larynx.*—The external laryngeal supplies the crico-thyroid; and section of this branch causes a hoarseness of voice from laxity of the vocal cords. This branch comes from the vagus; intracranial stimulation of the nerve causes contraction of this muscle. The recurrent laryngeal branch supplies all the other laryngeal muscles (this branch is derived originally from the spinal accessory). After its section there is complete aphonia, but in some cases sharp cries can be produced (Sedillot) by the action of the crico-thyroids.

(3). The smooth muscles of the bronchial tubes: the contractility of their walls has been proved by the experiments of Williams and Bert.

Other more doubtful contractions have been reported by some to result on stimulation of the pneumogastric; of the fibres of the spleen-capsule (Oehl); of the uterus (Kilian); of the bladder (Stirling).

Cardio-inhibitory function.—This has been already described in the chapter on circulation.

Vaso-motor function.—This action is very obscure. Stimulation of the peripheral end causes an increase of blood pressure (Heidenhain), with slowing of the velocity of the current; section of the nerves causes lowering of the blood-pressure (v. Bezold).

Excito-reflex action. (a) *In deglutition.*—Reflex movements of deglutition have been observed to follow stimulation of the superior laryngeal, and other branches of the vagus. The movements of the stomach, which commence on introduction of food, are due to stimulation of this nerve.

(b) *Influence of the pneumogastric on the respiratory movements.* Section of the vagi nerves is followed by slowness of the respiratory movements. The number diminishes even to half or one-fourth the normal; the inspirations are deep and laborious; and the length of the expiratory pause is greatly increased. But the slowness is compensated for by the increased depth, so that as much air passes into the lungs as before section (Rosenthal). After some time there is a diminution in the exchange of gases, with deeper color of the blood and lowering of temperature. This slowing of the respiratory movements does not occur in cold-blooded animals, such as the frog (Moreau).

Some animals die almost immediately after section of both pneumogastric nerves, but life is generally prolonged for some days (generally two to six for older dogs and rabbits, while the young succumb in one or two days). After death the lungs are found congested, with patches of broncho-pneumonia, and an excess of mucus collected in the bronchial tubes. These changes have been attributed by Frauler to the passage of particles of food into the air passages, but they have been seen by Cl. Bernard, when a tracheotomy tube had been introduced to prevent such accident.

Section of one vagus affects the respiratory movements on the affected side only, and does not tend to produce a fatal result.

Section of the recurrent laryngeal nerve produces dyspnoea, with laborious inspiration from paralysis of the laryngeal muscles.

(c) *Stimulation of the central end of the divided pneumogastric*

nerve gives different results according as the section has been made above or below the origin of the superior laryngeal. If below, a weak current produces quickening of the respirations, while a strong current causes tetanic contraction of the inspiratory muscles and cessation of the respiratory movements, which may last for more than thirty seconds.

When the stimulus is applied above the origin of the superior laryngeal, or to the latter branch itself, a weak stimulus produces slowing of the respiratory movements, while a strong causes tetanic contraction of the expiratory muscles, accompanied by relaxation of the inspiratory, so that respiration is arrested, with the chest contracted to the utmost.

According to these experiments the vagus trunk contains two kinds of centripetal fibres which act on the respiratory movements: *pulmonary* branches which stimulate the inspiratory centre and inhibit the expiratory, and *laryngeal* branches which have directly the opposite action on both centres (Rosenthal, Traube, Eckhard, &c.).

The above results have been contradicted by Bert, who affirms that the point of application of the stimulus is indifferent; weak stimulation in every case causing increased rate of the respiratory movements, and strong stimulation slowness, while arrest was in all cases produced by very strong stimuli.

Reflex action on secretions.—Stimulation of the central end of the vagus causes increase of the submaxillary secretion (Oehl); this does not occur if the chorda tympani have been previously divided. Arrest of the pancreatic secretion is produced by the same stimulation (Bernstein).

Reflex vaso-motor action.—Stimulation of the superior laryngeal and of the vagus trunk causes vascular constriction and an increase of the blood-pressure; of the depressor, as we have already seen, gives the opposite results.

Direct secretory action of the pneumogastric. (a) *Gastric Juice.*—This shall be studied with the digestive functions.

(b) *Renal Secretion.*—No action on this secretion could be made out by Eckhard; Cl. Bernard, however, found that on section of the vagi nerves the alkaline urine of the rabbit became acid. Galvanisation was found to cause increase of the renal secretion.

Action on the Liver.—Stimulation of the pneumogastric causes an increase of the hepatic *glycogen* and *glucose*, while

section of both nerves in the neck causes them to disappear completely (Cl. Bernard). *Glycosuria* also follows stimulation of the central end of the nerve according to the same observer.

Anastomoses. (1) *Auricular branch* (Arnold's nerve).—This branch, small in man, large and very sensitive in the horse and ox (Cl. Bernard), is chiefly composed of sensory fibres, passing from the pneumogastric to the facial, and, according to some authorities (Sappey, Valentin), contains motor fibres passing from the facial to the pneumogastric. It also contains vaso-motor fibres passing to the vessels of the ear; stimulation of the central end produces, first narrowing and then dilation, of the vessels of the auricle.

(2) With the *glosso-pharyngeal*.—This communication has been already noticed.

(3) With the *spinal accessory* from the ganglion of the trunk (plexus ganglioformis of Willis). This shall be again referred to.

(4) *Between the second ganglion and the superior cervical ganglion of sympathetic*.—This connection probably furnishes vaso-motor fibres to the vagus.

(5) *Between the second ganglion and the hypoglossal nerve*.

(6) *Between the pharyngeal branch and the glosso-pharyngeal*.—This aids in the formation of the pharyngeal plexus.

(7) *Between its terminal branches and the sympathetic*.—There are many of these communications: in the pharyngeal, cardiac, pulmonary, œsophageal, and cardiac plexus.

(8) *Anastomosis of Galen*.—The sensory fibres of the trachea and large bronchi pass from the superior laryngeal nerve along this communication to the inferior laryngeal, and so to their distribution.

(III) SPINAL ACCESSORY NERVE.—*Motor function*.—This is a purely motor nerve. (1) Its *external branch* supplies (with the aid of the cervical plexus), the sterno-mastoid and trapezius muscles. (2) The internal branch sends some of its fibres to the ganglion of the root of the vagus, while the remainder join the lower part of the second ganglion. It supplies the motor filaments of the recurrent laryngeal, and, according to some authorities, of the superior laryngeal also. According to some (Bendz, Longet), it also provides a great part of the motor fibres of the pharyngeal plexus, but Chauveau found contraction of the upper part of the superior constrictor alone to follow upon stimulation.

Sensory function.—This nerve is sensory after leaving the cranium; the sensory fibres come from the communications with the vagus, and with the cervical nerves.

Anastomoses.—(1) *With the posterior branches of the cervical nerves.*—This, probably, furnishes sensibility to the accessory nerve.

(2) With the pneumogastric (already described).

(3) With the cervical nerves. These aid in the supply of the sterno-mastoid and the trapezius muscles.

Ninth cranial nerve.—(*Hypoglossal; motor lingua*). **Motor function.**—This nerve is exclusively motor at its origin. It supplies the extrinsic lingual muscles, the genio-hyoid, and the thyro-hyoid. Accordingly, section of the nerve causes loss of the voluntary movements of the tongue, and makes deglutition very difficult. The apparent supply of the infra-hyoid muscles from this nerve is more than doubtful, the so-called *descendens noni* being formed by the recurrent fibres of the communicans noni. Stimulation of the roots of the hypoglossal nerve, was found by Volkmann to cause no contractions in these muscles beyond a few very slight and occasional movements, so that there is little room for doubt that the whole supply is from the cervical nerves.

Sensory function.—The hypoglossal is insensible at its origin, but below the hyoid bone the sensibility is very acute; this is due to its anastomosis with the cervical nerves, and probably in part to the pneumogastric. According to Cl. Bernard it possesses recurrent sensibility from the fifth nerve. Luschka describes and figures a recurrent branch from the gustatory of fifth, which passes in through the anterior condyloid foramen to supply the sheath of the hypoglossal nerve.

Vaso-motor and trophic functions.—The branches which go round the walls of the occipital sinus, to the *circellus venosus hypoglossi*, internal jugular vein, and diploe, are probably derived from the superior cervical ganglion.

Anastomoses.—(1) With the superior cervical ganglion. (2) With the pneumogastric. This gives sensory fibres to the hypoglossal, and perhaps motor to the pneumogastric. (3) *Ansa hypoglossi*. This loop contains motor fibres from the communicans noni passing to their distribution, and sensory fibres which ascend to the hypoglossal nerve.

Nerves of the organs of circulation.

The functions of these nerves have been considered with the circulation.

Glandular nerves.

Pfüger describes and figures the terminations of the nerve-fibrils in the cells lining the acini of the salivary glands ; but the anatomical accuracy of his observations on this point has been questioned by most other observers. But, although this connection may be denied, still the experimental results obtained by others have shown the powerful influence of the nerves on the activity of the glands. The influence of the lachrymal nerve on the gland of the same name, of the chorda tympani and auriculo-temporal nerves on the salivary secretions, also of the sympathetic on the same, and other secretions, leave no room for doubt as to the direct action of the nervous system on the glandular functions.

The so-called *paralytic secretion*, which appears in some cases after the division of glandular nerves, and goes on without intermission, is somewhat hard to explain. In some instances it would seem to be due to vaso-motor paralysis, but in other cases this influence cannot be made out.

Reflex influence on secretion.—This is more obvious than the direct action. It will be studied with the different secretions. Besides the increase that is usually manifest, an inhibitory influence is sometimes seen to proceed from the nervous centres, as in the well-known phenomenon of the dryness of the mouth that occurs from extreme fear, &c.

Trophic nerves.

Whether a set of trophic nerve-fibres, separate from the vaso-motor, have a real existence, is a point still unsettled. The ocular lesions which follow section of the ophthalmic nerve, have been referred to the removal of this nervous influence. Other analogous changes observed are the atrophy of the testicle, which was found by Nelaton and Obolensky to follow section of the spermatic nerves ; the changes of nutrition in the lower limb (paleness and dryness of the skin, formation of ulcers, falling off of hairs and nails, necrosis of the phalanges, &c.), which follow section of the sciatic nerve (Laborde), &c.

In some cases, however, directly opposite results have been observed to follow nerve-section. Brown-Sequard found that the cicatrisation of wounds took place more rapidly on the side on which the sympathetic was divided; and Snellen, on introducing a glass bead, on each side, into the subcutaneous tissue of the rabbit's ear, and dividing the sympathetic on one side, found that on this side the wound rapidly closed up, while an abscess formed on the opposite side. Adelman found that division of the tibial nerve of the horse was followed by hypertrophy of the leg-bones, and the œdema observed by Ranvier to follow section of the sciatic nerve belongs to the same category of facts. Most of these changes might, however, be explained by purely vaso-motor influence.

SYMPATHETIC SYSTEM.

This system of nerves does not appear to have any influence on voluntary actions, but presides by its sensory, motor, glandular, and perhaps trophic, fibres, over the organic and vegetative functions of life. Its motor fibres are distributed to the smooth muscular tissues throughout the various parts of the body, and accordingly are almost limited to the blood-vessels and viscera. The sensory fibres are engaged in supplying the mucous membranes and viscera. Most of its important functions have been already alluded to.

This system of nerves consists of (a) a number of ganglia and (b) of the fibres connected with them. The ganglia may be conveniently divided into *central* and *peripheral*, of which the latter are found scattered here and there in the viscera, &c., while the former form a double chain, one part on each side of the spinal column, reaching from the upper part of the neck down to the coccyx. The opposite chains meet below at the *ganglion impar*, while the upper ends communicate in the pituitary body, according to Ribes, or at the naso-palatine ganglion, according to Cleland.

The *fibres* are of the non-medullated variety, but mixed up with the sympathetic fibres everywhere are some derived from the cerebro-spinal axis. In some situations the axis-cylinders possess no sheath of Schwann, only a few nerve corpuscles being found here and there on its surface.

The *ganglia* are each surrounded by a fibrous capsule continuous

with the epineurium, while intersecting processes, continuous with the perineurium and endoneurium, pass into the interior. In the meshwork so formed the ganglion cells are imbedded. They are *polar* or *apolar*; the latter being embryonic forms. The polar cells are variable in size, some being several times as large as others. Each is enclosed in a hyaline capsule, which is lined by a single layer of flattened, nucleated, endothelial cells. Sometimes there is more than one cell within a capsule. Each ganglion cell possesses a large nucleus, and proportionably distinct nucleolus (seldom two). Each polar cell is connected with one or more nerve-fibres. Some fibres pass through the substance of the ganglion without becoming connected with any of the contained cells. Each process of the ganglion receives an investing sheath of Schwann, prolonged from the hyaline cell-capsule, while the endothelial lining cells become continuous with its layer of nerve-corpuscles.

In the frog, Beale discovered peculiar cells (usually bipolar), one of the processes of which is found to be formed by two fibres, a *straight* and a *spiral*. The latter is generally thinner than the straight fibre; and, according to Arnold and Courvoisier, splits up into a branching network of fibrils on the surface of the ganglion cell. The straight passes into the interior of the cell, where, according to the authorities just named, its axis-cylinder is continuous with the nucleolus. One of these fibres, usually the spiral (Axel Key and Retzius), after twisting a few times round the other, parts company, and receiving a coating of myelin, becomes a medullated fibre.

Of the peripheral ganglia of the sympathetic, some present peculiarities which will be noticed in their proper place.

The central ganglia of the sympathetic are arranged in the form of two symmetrical chains, one on either side of the spinal column. There are usually three in the cervical region, twelve dorsal ganglia, four lumbar, five sacral, and one coccygeal (the *ganglion impar*), median in position, to which both chains converge.

The *cervical sympathetic* distributes the following branches:—

- (1) Vaso-motor fibres to the corresponding side of head and neck, and (with the aid of the first thoracic ganglion) to the upper limb on that side;
- (2) The accelerator fibres of the heart;
- (3) The dilator fibres of the pupil;

- (4) Secretory fibres for salivary and lachrymal glands ;
- (5) Fibres to the *musculus orbitalis* ;
- (6) Centripetal fibres which excite the inhibitory centre of the heart ;
- (7) Centripetal fibres which excite the vaso-motor centres ;
- (8) Vaso-dilator fibres for the walls of the buccal cavity (Dastre and Morat).

The *thoracic sympathetic*.—The most important branches of this part are the *splanchnic* nerves. They contain the following :—

- (1) Vaso-motor fibres for the abdominal organs ;
- (2) Fibres which inhibit the peristaltic movements of the intestines ; they are easily exhausted, and their influence is lost when the blood becomes venous (S. Mayer and V. Basch) ;
- (3) Motor fibres for the intestinal walls (Nasse) ; fibres to supply the muscular tissues of the walls of the bile ducts (Munk) ;
- (4) Fibres which inhibit the renal secretion (CL. Bernard) ;
- (5) Fibres of which the stimulation is followed by glycosuria ;
- (6) Centripetal fibres, stimulation of which causes arrest of the heart's action ;
- (7) Centripetal fibres, stimulation of which produces contraction of the arteries.

The *abdominal sympathetic* supplies the greater part of the viscera contained in its cavity: large intestine, spleen, bladder, uterus, ureters, &c., with motor and vaso-motor fibres.

The *supra-renal* capsules have been looked upon by some as forming essential parts of the sympathetic system, but their real function still remains unknown. According to Brown-Sequard they are specially related to the formation of pigment, of which they limit the amount, and which accordingly accumulates in the system after their removal. Extirpation is generally soon fatal ; but this is probably from the nature of the operation itself. In the *bronzed-skin disease*, with which Addison's name is associated, disease of the supra-renal capsules is often, although not always, present.

PHYSIOLOGY OF THE SPINAL CORD.

Structure.—The investing membranes of the spinal chord correspond to those of the brain, *dura mater*, *arachnoides*, and

pia mater. The dura mater is formed of a number of superimposed layers of white fibrous tissue. The bundles of each layer intersect those of the adjacent ones at angles more or less acute; those of the outer layers are more circular, while the inner layers have chiefly a longitudinal course. Between the lamellæ are networks of branched connective-tissue corpuscles, with lymphatic lacunæ between; and the inner surface is lined by a hyaline elastic membrane, which is covered by a single layer of nucleated endothelial cells. The outer surface is also covered by a layer of endothelial cells (Axel Key and Retzius). This membrane is freely supplied with blood-vessels and nerves.

The *arachnoid* membrane is made up of finely-felted lamellæ of connective-tissue bundles, with corpuscles between. The outer bundles are chiefly longitudinal, and on this surface are one or two layers of endothelial cells. The inner lamellæ are chiefly transverse in direction, and form a kind of fenestrated membrane (Klein), with elongated transverse meshes. On the inner surface is a single layer of endothelial cells.

The *pia mater* consists of two layers: an external, formed of longitudinal bundles of connective-tissue, and connected to the inner layer by a network of fine elastic fibres. The inner layer itself is formed by a meshwork of connective-tissue bundles. Either surface of the *pia mater* is lined by a single layer of endothelial cells.

Between the arachnoid and *pia mater* is a layer of spongy *subarachnoidal tissue*, formed by a loose network of fibres continuous with those of the fenestrated layer of the arachnoid (Axel Key and Retzius).

The *ligamentum denticulatum* stretches between the *pia mater* and arachnoid, along the whole length of the cord, and forms a shelf on each side, dividing the subarachnoid space into anterior and posterior compartments.

In front, a dense band forms Haller's *linea splendens*, while the prolongation of the *pia mater*, from the lower end of the cord to the coccyx, forms the *filum terminale*, described by Macartney.

Between the dura mater and arachnoid is the *sub-dural space*; between the arachnoid and *pia mater* is the *subarachnoid space*. These spaces do not communicate with one another (Axel Key and Retzius).

The **spinal cord** (*medulla spinalis*) reaches from the occipito-atlantoid articulation to the interval between the first and second lumbar vertebræ. It is almost cylindrical in outline, but is somewhat flattened on the anterior and posterior surfaces, and presents swellings opposite the origins of the plexuses (*brachio-rachidian* and *lumbo-rachidian bulbs*).

Along the middle line in front is the *anterior median fissure*, which dips in for about one-third the antero-posterior diameter of the cord, and is filled by a process of pia mater. The so-called *posterior median fissure*, which passes in somewhat more deeply behind, is merely a septal process of neuroglia. Between the two median fissures is the *commissure*, which connects the lateral halves of the cord.

A transverse section of the spinal cord shows the position of the fissures, and the division of the halves of the spinal cord into columns: anterior, middle (lateral), and posterior. The white matter is placed externally, and forms the anterior part of the transverse commissure. The grey matter is arranged in the form of two crescentic masses; the convexities of which are placed back to back, and connected by the grey commissure. Their extremities are called *cornua*. In the commissure is the *central canal* of Stilling, which divides it into two parts, an anterior and a posterior.

The central canal is lined by ciliated columnar epithelium. It diminishes in size with advancing years, and varies in shape from above downwards, generally corresponding somewhat to the varying diameters of the cord itself. According to Stilling the transverse diameter in the dorsal region is .1 mm., while the antero-posterior is about .045 mm. The varying outlines of the canal, in transverse section, according to Lenhossek, are as follows: a little below the ventricle of Arantius it forms an antero-posterior slit; in the cervical region a triangle with the base forwards; in the dorsal region a circle; in the upper lumbar region a transverse slit; in the lumbo-rachidian bulb a rhomb; in the conus terminalis an antero-posterior slit, as at the upper end.

Microscopic examination shows the white matter to be formed by medullated fibres, not possessed of a sheath of Schwann, and mostly arranged longitudinally. A few are oblique or horizontal in direction. The horizontal fibres are found in the following situations:—

(a) In the anterior commissure, which is formed of medullated fibres, horizontally placed, connecting the anterior cornu of grey matter on one side, with the white matter of the anterior column of the opposite side (Gerlach). (b) Passing from the side of the anterior cornu of grey matter, horizontally outwards, to the white matter of the lateral column of the same side. (c) Emerging from the posterior cornu, and similarly passing to join the white matter of the posterior column. They probably become continuous with the fibres of the posterior roots of the spinal nerves. (d) The fibres of the posterior roots are placed horizontally, for some distance after entering the cord, before entering the posterior cornu of grey matter.

The *grey matter* is made up of ganglion cells and nerve fibres, imbedded in the peculiar connective tissue (*neuroglia*). This tissue is made up of the characteristic matrix, fibres, and cells already described. The anterior cornu, which is blunt and serrated, contains three groups of ganglion cells: (1) an *anterior*; (2) an *external*; and (3) an *internal*. In the dorsal region there is a group about the middle of the concave edge of the semilunar mass: the *tractus intermedio-lateralis* of Lockhart Clarke. In the posterior horn the ganglion cells are found in small groups in the anterior part, and as isolated cells in the posterior part.

The processes of the ganglion cells are of two kinds: the *axis-cylinder*, and *protoplasm*, as described by Deiters, the peculiarities of which have been already mentioned. The unbranched axis-cylinder process is found only in the cells of the anterior cornu (Gerlach). There are sometimes two, although but one as a rule. After some distance this process receives a medullary sheath, and passes into an anterior nerve-root. The protoplasm processes branch and enter a network (Gerlach's *nerve-plexus*), formed by the primitive fibrillæ. In this plexus the fibrils of the posterior roots probably communicate (indirectly) with the protoplasmic processes.

Of the nerve-fibres of the grey matter, many varieties may be defined: (a) the fibres of Gerlach's plexus, already mentioned; (b) longitudinal medullated fibres which may be traced in from the anterior roots, and turn up to the brain (Kölliker); (c) fibres which originate in Gerlach's plexus, and pass up to the brain as longitudinal fibres; (d) fibres origina-

ting in the nerve-plexus of the anterior horn, cross in the anterior commissure, and ascend in the anterior white columns of the opposite side; (*e*) bundles of fine non-medullated fibres pass through the grey commissure to the opposite side; (*f*) horizontal fibres are found in large numbers in the anterior part of the posterior cornu; (*g*) a large bundle of longitudinal fibres is found about the middle of the posterior cornu, and receives fibres both from the posterior white column and from the posterior nerve-roots; (*h*) from the tractus intermedio-lateralis (in the dorsal region), numerous fibres arise which, according to Gerlach, form three bundles, one of which passes backwards, while the other two pass outwards, intersecting one another as they proceed; (*i*) the posterior root-fibres which enter the posterior cornu run upwards or downwards for a variable distance, and are then lost in Gerlach's nerve-plexus.

In the posterior part of the posterior cornu of grey matter, an accumulation of neuroglia-tissue forms the *substantia cinerea gelatinosa* of Rolando. A zone of neuroglia also surrounds the canal of Stilling (the *central grey nucleus* of Kölliker). This contains a few small ganglion cells (Gerlach).

Spinal Centres.

The situation and functions of a certain number of centres of the spinal cord have been determined with sufficient accuracy.

(1) *Cilio-spinal centre*.—This centre, which presides over the dilatation of the pupil, has been found to reach from the sixth cervical to the fourth dorsal vertebra (Waller, Budge, Francois-Franck, &c.).

(2) *Accelerator centre of the heart*.—The situation of this centre has been already considered.

(3) *Respiratory centre*.—This has been placed at the *calamus scriptorius*. It is found that removal of the brain and medulla from above this level, if done with sufficient care, does not cause arrest of the respiratory movements; nor does removal of the spinal cord from below by successive slices, as the facial respiratory motions still persist. But removal of this part alone of the nervous axis immediately stops all respiratory action.

(4) *Centres of the movements of the limbs.*—The reflex movements of the limbs, which remain after section or injury of the spinal cord, leave no doubt of the importance of the influence exercised over these movements by the spinal centres. The localisation of these centres still remain, however, very imperfect (Haleß, Cl. Bernard).

(5) *Genito-spinal centre.*—At the level of the fourth dorsal vertebra in the rabbit, Budge found a region of a few lines in length, stimulation of which caused movements of the lower part of the rectum, of the bladder, the vasa deferentia, and, in the female, of the uterus. Segalas had, after division of the lumbar part of the cord, produced erection and ejaculation of semen by mechanical irritation of the lower segment. Goltz and Freusberg have found, after section of the spinal cord at the level of the first lumbar vertebra in the bitch, that rut, pregnancy, parturition, and lactation took place as if nothing had happened.

Goltz has found that the centre of erection is placed in the lumbar part of the spinal cord; after section of the cord above this level, titillation of the penis produced erection, with rhythmic movements of the pelvis; the erection failed to appear after destruction of the lumbar part of the cord. It is also checked by stimulation of the sciatic nerve, by galvanisation of the skin of the scrotum or anus, or even by pressure on the toes.

(6) *Ano-spinal centre.*—Masius has found that in the rabbit, between the sixth and seventh lumbar vertebræ, a centre exists, stimulation of which produces movements of the sphincter ani. In the dog, after division of the lumbar cord, introduction of the finger into the anus produces rhythmic contractions which are arrested by strong stimulation of a sensory nerve, as by pressure on the toes (Goltz).

(7) *Vesico-spinal centre.*—Irritation of the spinal cord at the level of the third lumbar vertebra (or of the vesical sympathetic filaments) is followed by feeble contractions of the body and neck of the bladder; stimulation of the cord at the fifth lumbar vertebra, or of the spinal vesical nerves, causes energetic and painful contractions (Gianuzzi). According to Goltz, micturition is a purely reflex act of which the centre is placed in the lumbar cord. After division of the cord above this part, micturition immediately follows when the anus is tickled, or when

the glans penis or prepuce is touched with the finger, or when pressure is made on the skin of the abdomen. This reflex act does not follow when the lumbar part of the cord has been divided.

(8) *Vaso-motor centres*.—These have been already noticed at sufficient length.

(9) *Centre of cutaneous secretion, and inhibitory centre of same*.—These we shall consider with the physiology of the skin and its glands.

(10) *Centres of muscular tonicity*.—This function of the cord has been already alluded to.

Other nerve functions which have been referred to the cord are the following :—

Trophic influence.—The influence of the cord on the nutrition of the anterior roots of the nerves is shown by the degeneration which ensues upon pathological changes in the corresponding part of the cord, as well as by the results of section.

Influence on absorption.—Goltz has found that, after destruction of the spinal cord, absorption of a solution of common salt injected into the lymph-sacs of the frog takes place very slowly, while it takes place rapidly in the healthy animal.

Influence on the temperature.—This shall be studied with animal heat.

Psychical action.—Acts of apparent consciousness are sometimes attributable to the influence of the spinal cord alone, as the following experiments seem to show. *Pflüger's*.—A drop of acid is placed on the upper part of the thigh of a decapitated frog; the animal is seen to bend the limb and try to wipe it off. This leg is then amputated, and another drop is placed on the same spot; when, after making some ineffectual attempts with the amputated limb, it wipes off the acid with the opposite foot. *Auerbach's*.—The leg of a decapitated frog is amputated, and a drop of acid is placed on the back on the same side, when, after making some efforts to remove it with the amputated limb the animal remains motionless. Another drop of acid is then placed on the back of the opposite side, the animal rubs it off with the intact limb, and then proceeds to rub the irritated spot on the opposite side with the same foot. These results are not constant, but occur pretty often, and would seem to indicate the existence of a rudimentary consciousness. Still many look upon these actions as purely reflex.

The cord, also, has some different and peculiar nervous actions in a peculiar way. Brown-Sequard found that section of a lateral half of the spinal cord of the guinea-pig at the level of the twelfth dorsal vertebra was followed by localised analgesia in a limited region of the side of the face and neck. It was also found that stimulation of this region of the skin produced epileptiform convulsions (*zon e epileptogène*), and that these convulsions could even be transmitted to the young of the animal.

Transmission of impulses along the cord.

The paths by which the various forms of nervous action

pass along the spinal cord have been studied by experimental section, and by observing the results of pathological lesions.

Posterior columns.—Section of the posterior columns produces neither motor nor sensory paralysis. According to Brown-Sequard it is followed by cutaneous hyperesthesia on the corresponding side below the level of the section, but Ott and Meade say that this result occurs only when the grey matter is implicated in the lesion. According to Schiff, tactile sensations properly so-called are transmitted along these columns. After section of the whole thickness of the cord, excepting the posterior columns, sensibility to contact remained, while sensibility to pain was entirely abolished. Successive transverse sections of these columns at different levels (Todd's experiment) cause symptoms like those of *locomotor ataxy*, but it cannot be determined whether they are due to the lesion of the fibres which preside over the muscular sensibility, or of those which co-ordinate the tactile sensations induced by the movements of walking.

Lateral columns.—Complete section of the lateral columns is followed by loss of voluntary motor power, cessation of the respiratory movements, and, according to some, loss of cutaneous sensibility and muscular sense. According to Schiff, however, sensibility is retained; Ott and Meade have found it somewhat diminished. After section of the cord, excepting the lateral columns, voluntary movements, reflex movements, and tactile sensibility remains, only the movements are found to be ataxic. The lateral columns, accordingly, seem to form the paths along which are transmitted voluntary motor fibres, also respiratory, vaso-motor, cilio-spinal, perhaps tactile fibres, and those which preside over muscular sense.

Anterior columns.—Section of the anterior columns alone is nearly impracticable, and accordingly the function of these columns remains in great obscurity. It is believed by some authorities, that these columns transmit the inhibitory fibres by which the encephalon controls spinal reflex movements. It has been found that after section of the anterior half of one segment of the cord, voluntary motion and sensation were still preserved.

Grey matter.—After complete division of the columns of grey matter voluntary motions are still preserved. The alterations of sensibility have been variously described. According to Schiff, sensibility to pain is abolished (*analgesia*), while the tactile sensibility is retained. Section of the posterior cords with the grey substance, on the other hand, causes complete abolition of sensibility. According to the same observer, after complete section of the white substance of the cord, motor power remained when the grey matter continued intact, so that it would seem to act as a conductor of motor impulses. Some careful observers, however (Ott, Meade, &c.), deny the existence of either motor or sensory fibres in the grey matter.

Transmission of sensibility.—According to Schiff and Danilewsky, sensations of pain and of temperature are transmitted chiefly by the grey substance, and tactile sensibility by the posterior columns. The latter is said, however, by Woroschiloff, and some other recent observers, to travel in the lateral

columns ; and, similarly, the muscular sense. Brown-Sequard makes the different forms of sensation to pass along separate paths. The anterior part of the grey matter transmits tactile sensations ; impressions of pain (more widely diffused) pass by the lateral and posterior parts ; and those of temperature by the central : all crossing in the cord. Muscular sensibility, on the other hand, travels by the anterior cornu, or in its neighbourhood, and does not cross.

A partial transverse section of one half of the spinal cord causes a diminution of sensibility on the opposite side, better marked according as the section extends more deeply, and extending uniformly over the surface. Complete transverse section of one half of the cord causes complete anæsthesia of the opposite side, accompanied by hyperæsthesia of the corresponding side. This hyperæsthesia exists not only in the skin, but in the articulations, periosteum, &c., (Koch). It is attributed by Brown-Sequard to paralytic distension of the blood-vessels ; by Ludwig and Woroschiloff to section of the inhibitory fibres connected with the encephalon. If a vertical antero-posterior medium section of the cord be made, so as to separate it into two lateral halves, bi-lateral anæsthesia results, engaging the cutaneous surface which receives its sensory fibres from the part of the cord operated on. These facts seem to demonstrate the crossing of the sensory fibres, but some contradictory results have been reported. According to Van Deen, if the lateral halves of the cord be transversely divided at different heights, sensibility is preserved on the two sides.

Transmission of motor impulses.—The fibres which transmit voluntary motor impulses pass along the pyramidal bundles of the lateral columns, and perhaps along the column of Turck. According to Schiff, the grey substance is also engaged. The respiratory, cilio-spinal, and vaso-motor fibres also pass along the lateral columns.

The transmission of motor impulses is also direct: transverse section of one lateral half causes abolition of voluntary motion on the same side (*acinesia*), and a longitudinal section separating the two halves does not affect voluntary motion at all. Vulpian, however, believes that there is a partial decussation in the white substance ; he has found stimulation of the anterior column produce active movements on the corresponding side, and feeble movements on the opposite.

Transmission of reflex action.—The fibres which preside over the transmission and co-ordination of spinal reflex actions appear to pass in the posterior columns, in the anterior part of the lateral, and, it has been supposed by some, in small numbers in the anterior columns, and in the grey substance.

Inhibition of reflex action.—The fibres which transmit the impulses that inhibit reflex actions are chiefly, if not solely, placed in the anterior columns.

Reflex actions of the spinal cord.

The general nature of reflex action has been already studied ; from which we can understand that the essential condition necessary for reflex action is the intervention of one or more nerve-cells between the sensory and motor fibres. Accordingly, reflex action is produced in isolated segments of the spinal cord. The initial stimulus may be applied either to the sensory or sympathetic ; pinching the sympathetic in the rabbit causes contractions of the abdominal muscles (Volkmann). Stimulation of the intestinal canal causes movements, which cease as soon as the spinal cord is destroyed. As a rule, the anterior roots are in communication with the posterior roots of the nerves on the same side, and the reflex movements correspond. Under certain conditions, especially when the reflex centres are in the medulla oblongata, the movements are on the opposite side (*cross reflex*).

Cayrade, who contradicts Pflüger's laws, asserts that reflex stimulation radiates in all directions along the spinal cord, and as easily upwards as downwards.

Reflex irritability is increased by decapitation, and, generally speaking, by any cause which removes or diminishes the activity of the cerebral influence. It is accordingly increased by ligation of the arteries, and successive transverse sections of the cord from before backwards, increase the irritability behind the seat of division. Of two frogs of equal strength, one was decapitated, while the cord of the other was divided in the lumbar region : the reflex movements were stronger in the latter.

Reflex irritability is increased by strychnia, by brucia, by carbolic acid, curara, caffeine, opiates, &c. Cl. Bernard believed that these drugs acted on the sensory nerve roots, while Vulpian

supposes that they act directly on the spinal cord. It is diminished by aconite, chloral hydrate, bromides, hydrocyanic acid, æther, and chloroform. The action of electricity has been variously described; according to Legros and Onimus ascending currents produce an increase, and descending currents a diminution, of reflex movements, but these results have been contradicted by Upenstrenki.

The *time* occupied by the reflex transmission in the cord (*time of reflection*) diminishes with the intensity of the stimulus; this makes a point of difference between transmission in the cord and transmission in the nerves.

The *mechanism* of the reflection is not definitely known, but probably corresponds to the hypothetical scheme already described. Marshall Hall postulated the existence of a distinct set of fibres, to which he gave the name of *excito-motor*, whose special function it was to perform the reflexion.

Inhibition of reflex action.—Stimulation of the *cortex cerebri* (Goltz), or of the *tubercula quadrigemina* (Setschenow), causes a diminution and suspension of the reflex phenomena of the cord. On this ground Setschenow has supposed the existence in the grey substance of the encephalon, of centres which inhibit the reflex action of the cord. Powerful stimulation of sensory nerves diminishes or paralyzes reflex action (Lewison); this stimulation probably acts on the inhibitory centres. Special-sense nerves have the same inhibitory influence (Langendorff, Böttcher). According to these authorities, section of a large sensory nerve such as the sciatic, or of the optic or auditory nerves, has an influence on reflex action, similar to decapitation. Nothnagel admits the existence of sensory nerves throughout the whole length of the cord, and there is no doubt that the stimulation of the sensory nerves above referred to, does not act on the intracranial centres alone, for it has been found to control reflex action in dogs, after division of the cord in the lumbar region.

Goltz attributes this inhibitory influence to the diminution of excitability, which results when two stimuli arrive simultaneously at an inhibitory centre, from separate sensory nerves. Cyon believes that a true interference of the waves of stimulation takes place. Schlosser supposes that the phenomena of inhibition are due to antagonistic movements, which prevent the reflex movements from taking place.

PHYSIOLOGY OF THE BRAIN.

The determination of the functions of the different parts is a problem which is attended by difficulties, and which has remained in great obscurity till within the last few years.

The following proceedings have been adopted for the purpose of determining the functions of the encephalon :—

Stimulation. (1) *Pricking.*—This is done by exposing a part of the central mass, and pricking with a fine needle to a greater or less depth. When stimulation alone is required, care is taken not to lacerate any part of the cerebral substance. (2) *Electrisation.*—This is done by constant or interrupted currents, and more especially by induced currents. (3) *Hyperæmia and inflammation.*—These phenomena are produced by irritation of the cerebral substance by application of irritating substances, by pricking, &c.

Abolition of function. (1) *Section.*—This proceeding is adopted for the purpose of interrupting the continuity of nervous transmission, motor or sensory, especially the former. (2) *Ablation or destruction.*—Removal with a bistoury, or destruction by the actual cautery, is adapted for the removal of superficial parts of the brain substance. (3) *Injection of caustic solutions.*—This method, which was first adopted by Beaunis, and, subsequently, by Nothnagel and Fournier, has the advantage of enabling the observer to reach the deep parts without serious injury to the superficial. (4) *Interstitial aspiration.*—This method was also adopted by Beaunis, and is done by using an exhausting syringe, the nozzle of which is attached to a fine canula introduced into the brain substance. Sudden withdrawal of the piston causes rupture of a number of capillaries, and a hæmorrhage more or less localised. (5) *Method of Goltz.*—This consists in the removal, by a current of water of sufficient strength, of a portion of the cortex cerebri. Two openings are trephined in the skull, and a canula is introduced through one opening and directed obliquely towards the other. When passed a short way into the cortical substance, a stream of water, directed with sufficient force through the canula, washes out the brain tissue through the second opening. In this way, any requisite area of the cerebral hemispheres may be decorticated. (6) *Electrolytic cauterisation* has also been employed by Beaunis. (7) *Interruption of the circulation.*—This may be effected by deligation of the blood-vessels, or, for limited regions, by injection of pulverised substances, such as lycopodium powder, &c. (*experimental embolism*). (8) *Refrigeration* (Richardson).—This is done by the use of the æther spray, application of ice, &c., causing temporary suspension of the functions of the part; but the great objection to the method is the impossibility of localising the effect. (9) *Compression.*—This is effected on the surface by direct pressure; in the deeper parts, by the injection of harmless fluids.

Medulla oblongata.

The irritability of the different parts of the medulla oblongata is very differently described. Stimulation of the anterior pyra-

mids causes movements without signs of pain (Longet); signs of pain have been observed by Vulpian. The restiform bodies and posterior pyramids, on the other hand, have been found very sensitive by Longet and Vulpian, while Brown-Sequard considers them to be nearly void of sensibility.

Nervous centres in the medulla.—(1) The respiratory centre is placed at the level of origin of the pneumogastric nerves, near the point of the *calamus scriptorius*. It is composed of two parts: an *inspiratory* and an *expiratory*. (a) The *inspiratory centre* is stimulated by irritation of the sensory nerves, cutaneous as well as pulmonary, by the accumulation of carbonic acid in the blood (dyspnœa), by the absence or diminution of oxygen, or by elevation of temperature (heated blood). Its activity is, on the other hand, diminished or paralysed by stimulation of the sensory nerves, especially those of the heart (stimulation of the endocardium, Francois-Franck) by excess of oxygen (apnoea) or of carbonic acid (asphyxia) in the blood, and by increase of the intracranial pressure. The activity of this centre is intermittent (or rhythmic) like that of the heart. (b) The *expiratory centre* is only called into play on special occasions, for ordinary expiration is purely passive. It is excited by irritation of many sensitive nerves, and especially of the branches of the superior laryngeal.

These respiratory centres appear to be bilateral; for longitudinal division of the cord into its two lateral halves does not stop the respiratory movements, but transverse section of one half paralyses the respiratory muscles on that side. According to Gierke and Heidenhain the centre is not formed by a mass of grey matter, but by a simple white cord descending on each side from the roots of the trifacial, glosso-pharyngeal, pneumogastric, and spinal accessory nerves. This fasciculus descends to the brachial enlargement, and is there connected with its fellow of the opposite side by transverse fibres. Removal of a circumscribed mass of the nervous substance at the nib of the *calamus scriptorius* (*nœud vital* of Flourens), causes instantaneous stoppage of the respiratory movements. Section of the medulla below this point causes cessation of the respiratory movements of the trunk, while those of the face (movements of the *alæ nasi*) persist; section above the *nœud vital* stops the respiratory movements of the face, while those of the trunk persist. The immediate death which follows its

extirpation, has been attributed by Brown-Sequard to arrest of the heart's action.

This is generally included among the automatic centres, as the stimuli which determine its activity are always acting during the normal state. Its activity has been said to persist after section of all the sensory nerves connected with it, but the experiment has given opposite results in the hands of Rach and Von Wittich, and it is probable that stimuli are always travelling towards it from the periphery, which determine the emission of the impulses. Connected with the respiratory centre, are the centres of sneezing and of coughing. According to Koch, the latter is placed immediately above the respiratory centre.

(2) *Vaso-motor centre*.—See page 191. The existence of a vaso-dilator centre has been supposed by some.

(3) *Centre for dilatation of the pupil*.—According to the researches of Schiff and Salkowski, this centre should be placed in the medulla, and not in the cilio-spinal region.

(4) *Cardio-inhibitory centre*.—See page 188.

(5) *Centre for movements of deglutition*.—Lesions of the medulla cause paralysis of the movements of deglutition, but the exact situation of the centre has not been determined. After section or removal of the parts immediately above the medulla, deglutition is still performed when a bolus is placed on the back of the tongue.

(6) *Centre of phonation*.—If the brain be removed from above the medulla, the animal so treated still cries when hurt (Vulpian). The medulla influences the expiratory movements and the muscles of the vocal cords. Dugès and Schroeder van der Kolk would localise the centre in the olivary body, but this conclusion is not borne out by sufficient evidence.

(7) *Glycogenio (diabotio) centre*.—It was discovered by Claude Bernard that temporary *glycosuria* follows puncture of a certain spot in the floor of the fourth ventricle (the tubercle of Wenzel, which includes the origins of the auditory and pneumogastric nerves). If the puncture be made a little higher up, albuminuria results, and if a little lower down, polyuria.

(8) *Centre of vomiting*.—The localisation of this centre is still undetermined.

(9) *Sudoriparous centres*.—Their position has not been made out. They must be bilateral, for sweating confined to one side

has been observed in certain obscure conditions. Centres of inhibition of the secretion are believed by Vulpian and by Ott to be also situated in the medulla.

(10) *Centre of co-ordination of reflex movements.*—If in the rabbit the medulla oblongata be divided 6 mm. above the calamus scriptorius, generalised reflex movements are still performed; but if the section is placed only a millimetre lower down the reflexes are but partial (Owsjannikow).

Transmission of nerve impulses.—*Sensory.*—Physiologists have failed to determine the paths of transmission of sensory impulses in the medulla. Longuet asserted that loss of sensation followed section of the restiform bodies, but this has been disproved by other observers. Whether the paths are direct or crossed has not been well made out, but it has been found that separation of the medulla into its two lateral halves does not materially affect cutaneous sensibility. It is probable that the course is in the grey matter of the medulla, and for the most part, at least, directly upwards without crossing.

Motor impulses.—Motor transmission is chiefly along the anterior pyramids, and probably by the fasciculus intermedius. The path is crossed. The decussation takes place in the medulla for the muscles of the trunk and limbs; for those of the face it is in the protuberance. In man the decussation is usually complete, but there are individual variations, as pathological lesions prove (Charcot); in other animals, on the contrary, it is always partial and hemisection of the medulla does not cause complete hemiplegia on either side. According to Lussana and Lemoigne, the decussation of the motor fibres takes place much higher up.

Pons Varolii.

Stimulation of the superficial part of the pons gives no result except the irritation is applied to the middle peduncle (*vide cerebellum*); when the deep (posterior-superior) surface of the pons is reached, pain is manifested. Irritation of the central part of the pons causes epileptiform convulsions.

Transmission of impressions. *Sensory.*—According to Brown-Sequard, sensations (of contact, temperature, pain, muscular sense, &c.) pass in the deep part of the pons. Lesions of one

side of the pons cause anæsthesia of the opposite side of the body.

Motor.—Motor transmission takes place chiefly in the anterior (superficial) part of the pons. Unilateral lesions of the pons cause acinesia of the trunk and limbs on the opposite side and of the face on the same side (Gubler's *alternate hemiplegia*), because the facial nerve-fibres decussate in the pons.

In the pons the following centres are located by recent authorities :—

- (1) *Centres of facial expression ;*
- (2) *Centres of mastication and of suction ;*
- (3) *Centres of movements of the eyelids ;*
- (4) *Centres of movements of the eye-balls.*—It has been shewn

by the experiments of Duval and Laborde that a centre of association of the movements of the eyes for binocular vision is found at the level of the nucleus of origin of the sixth nerve. Stimulation of this region causes conjugate deviation of the eye of the same side, and its destruction causes conjugate deviation of that of the opposite eye ; while destruction of the nuclei of both sides causes convergent strabismus. These phenomena are due to the fact that the nucleus, besides forming the origin of the sixth nerve on the same side, sends some fibres to the third and sympathetic of the opposite side. In consequence of this distribution the co-ordination of the ocular muscles is preserved, so that the internal rectus of one side can move simultaneously with the external rectus of the opposite.

(5) *Centre for station and for locomotion.*—When the pons is left after the removal of the upper part of the brain, the animal is able to stand straight, and even to walk, although with a staggering gait ; but, after removal of the pons, no attempt at locomotion is made.

Lussana and Lemoigne have found retrograde movements to follow stimulation of the fasciculi teretes in the floor of the fourth ventricle, while their division on each side of the middle line paralysed these movements. Accordingly, they have advanced the idea that a *centre of recoil* is present in this situation.

(6) *Centre for the general movements of the limbs*—After the removal of all parts of the encephalon above the pons, the movements of all four limbs can still be executed with energy and co-ordination.

(7) *Convulsive centre*.—Galvanisation of the pons has been found to produce epileptiform convulsions, and the limits of the *region of cramps*, or *convulsive centre*, have been carefully defined by Nothnagel. This centre is stimulated by an excess of carbonic acid in the blood, by absence of oxygen (asphyxia), by anæmia, by contraction of the blood-vessels of the protuberance (Kussmaul and Tenner), by hyperæmia of these vessels (Landois), and by most cardiac poisons. The convulsive centre is in intimate relation with the respiratory, vasomotor, cardio-inhibitory, and that which presides over dilation of the pupil; this is shown by the phenomena of asphyxia, which throw all these centres into activity.

(8) The *salivary centre*.—The centre which presides over the salivary secretion appears to be placed at the level of origin of the facial nerve; pricking, or electric stimulation of this point, causes an abundant secretion of saliva (Cl. Bernard, Eckhard, &c.)

(9) *Centre of sensibility*.—The centre of sensation has been placed by Gerdy and Longet in the pons; they have found general sensibility remain after removal of all parts of the brain in front of the protuberance, while all manifestations of pain disappeared on its removal. This hypothesis is favored by Vulpian; but, according to Brown-Sequard, the movements of pain under these conditions are purely reflex.

(10). *Centres of inhibition of heat-production*.—These have been admitted by some authors to be present in the pons, but their influence is very obscure.

Crura Cerebri.

The *cerebral peduncles* are sensitive; stimulation produces signs of pain. They transmit voluntary movements and common sensations, and form the connecting link between the motor medullary centres below and the voluntary or reflex motor centres of the cerebral ganglia (corpus striatum, &c.) and of the cortex cerebri. Complete section on one side causes paralysis of motion (*acinesia*) and paralysis (or diminution) of sensation (*anæsthesia*) of the opposite side of the body. According to Wundt, section of the lower part of the crus (*crusta*) destroys voluntary motion, but reflex movements can still be produced, by stimulation of the sensory nerves. If

the section engages the upper part of the cerebral peduncles and the ribbon of Reil, reflex movements are destroyed, but voluntary movements persist (with ataxia and wavering gait).

Lesion of one cerebral peduncle causes a *circus movement* from the side opposite to the lesion; in this movement the animal describes a circle, of which the radius is smaller as the lesion approaches the upper edge of the pons and engages a greater number of fibres. In three cases of lesion of the upper and outer part of the crus, Beaunis has observed movements of rotation on the long axis of the body. *Divergent strabismus* and *mystagmus* have also been observed in some cases.

The *crusta* appears to be concerned in the transmission of voluntary movements and conscious sensibility, while the *tegmentum* transmits the reflex movements which depend on the ganglionic centres (corpus striatum, optic thalamus, &c.)

Lesions of the *internal capsule* produce different effects, according to the seat of the lesion. If the posterior third of the posterior segment be divided, loss of common sensation and of special sense (sight, hearing, &c.) on the opposite side is the result (*cerebral hemianæsthesia*). When the section is farther forwards at the genu of the internal capsule, motor paralysis of the opposite side of the body is the consequence (Carville, Duret). Pathological lesions have been found to produce the same results, according to their seat (Charcot and others).

Budge has seen contractions of the stomach, intestine, and bladder, follow stimulation of the cerebral peduncles. Afasanieff has reported an increase of the lachrymal and salivary secretions produced in the same way; while section was followed by dilation of the arteries on the same side. Danilewsky, experimenting on curarised dogs, has found increase of blood-pressure and slowness of pulse, produced by stimulation of the cerebral peduncles.

Corpora Striata.

Most physiologists agree that electric stimulation of the corpora striata causes general contraction of the muscles of the opposite side of the body; Gliky and François-Franck have, however, found opposite results. These authorities affirm that irritation of the grey matter produces no results, but that the

muscular contractions are produced by stimulation of the white fibres of the internal capsule.

Extirpation of the corpora striata has given contradictory results; perhaps on account of the varying amount of injury of the internal capsule. All experimenters, however, seem to agree, that the corpora striata form motor centres of a higher order than those situated in the spinal cord. In man, disease of the corpus striatum is always accompanied by motor paralysis on the opposite side, without any loss of sensation. When the pathological lesion does not reach the internal capsule, the acinesia is always temporary. Nothnagel has described in the striate body of the rabbit a *nodus cursorius*, the stimulation of which produces irresistible onward movements. Magendie, on the other hand, has described in the corpora striata a centre of recoil, ablation of which produces a tendency to an irresistible forward progression, while stimulation produces retrograde movements.

Thalamus Opticus.

Stimulation of the optic thalami causes neither pain nor special form of movement; the troubles observed in some cases appear to be due to stimulation of the cerebral peduncles, or of the anterior quadrigeminal bodies. *Extirpation* or destruction of these bodies has given but indefinite results. According to Nothnagel, neither motor nor sensory paralysis follows; and he is disposed to adopt the theory of Meynert, who makes these bodies the centres of the combined movements which are produced unconsciously, and by reflex action, from the impressions which pass to them from the peripheral sensory surfaces. Luys, however, would make them centres of sensibility, the common centre of reception (*sensorium commune*) for the various forms of sensory impressions (tactile, dolorous, olfactory, optic, acoustic, gustatory, genital, and visceral). The tactile centre, the largest, he places in the median part; the olfactory, optic, and acoustic, he places, from behind, forwards inside the tactile centre.

An inspiratory centre has recently been described by Christiani in the thalamus opticus, placed near the tubercula quadrigemina. Stimulation of this point, according to him, causes a deep inspiration, followed by quickened respiration, or arrest of respiration in the inspiratory stage.

Balogh has found quickening of the heart's action produced by stimulation of the upper part of the thalamus opticus, and slowing by that of the inferior portion.

Corpora Quadrigemina.

Stimulation of the corpora quadrigemina produces manifestations of pain, except when the irritation engages the superficial part only. Mechanical stimulation affects these bodies if the deep parts are engaged (Ferrier, Beaunis). Movements are produced by stimulation of these bodies, especially movements of the eye-ball and of the muscles of the limbs. According to Beaunis, application of chemical irritants produces no movements.

(1) *Vision*.—Removal of the tubercula quadrigemina produces immediate blindness, with fixed and dilated pupils (Flourens); while in the pigeon removal of all the parts of the brain in front of these bodies leaves obvious manifestations of remaining vision. Ferrier has observed similar phenomena in monkeys. Removal of these bodies on one side, causes blindness of the opposite eye.

(2) *Movements of the pupil*.—Flourens placed here the centre which presides over contraction of the pupil; basing his conclusions on the effects of removal of these bodies. But direct stimulation of the corpora quadrigemina usually produces dilation of the pupil (contraction appears only when convergence of the pupils occurs at the same time). According to Knoll, the dilating centre is placed in the anterior tubercles (*nates*), stimulation of which produces dilation of both pupils, especially that of the corresponding side; this dilation fails to appear after section of the sympathetic. According to Ferrier, stimulation of either anterior or posterior tubercles causes pupillary dilation, first on the *opposite* side, and afterwards on the same side.

(3) *Movements of the eye-ball*.—According to Adamük, stimulation of the anterior tubercle of the right side causes left-sided deviation of both eyes; if the anterior part alone be excited, the axes of vision are directed horizontally; if the median part be stimulated, the pupil dilates widely, and the axes of vision are directed upwards; if the stimulus is applied further back, this position is accompanied by convergence of the eyes; lastly,

if the extreme posterior part is stimulated, the axes of vision are directed downwards, and the pupil is contracted. In addition to these movements, Beaunis has observed either *protrusion* (exophthalmos) or *retraction* of the eye-ball follow stimulation of the quadrigeminal bodies; retraction seemed to take place when the stimulus was applied further back. Oscillatory movements of the eye-balls (*nyktasmus*) has been observed to follow lesions of these bodies.

Stimulation of the posterior tubercles (testes) causes various movements of the eye-ball, singly or associated: (1) *convergence* of the eyes, with (2) *internal rotation*; (3) downward movement of the eye-balls; (4) stimulation of the internal part of one posterior tubercle causes deviation of both eyes to the same side.

(4) *Movements of the head*.—If the stimulus be sufficiently strong, movements of the head result, corresponding to those of the eyes; and, in some cases, they may take place independently (Beaunis). The centre for movements of the head is then probably placed in the corpora quadrigemina, and close to that of the eye-balls, but less readily excited. In addition to these movements of the whole head, partial movements have been observed: of the eye-brows and eyelids, of the ear, of the upper lip, of the lower jaw, &c. (Ferrier).

(5) It was supposed by Serres that the tubercula quadrigemina preside over the equilibration of movements. Loss of power of re-establishing the equilibrium of the body has been found by Goltz to follow destruction of the optic lobes in the frog, and similar results have been obtained by M'Kendrick in case of birds and rabbits.

(6) *Movements of expression*.—Ferrier has found that irritation of the posterior tubercles caused expressions of pain of varying character. It has also been observed that most of the movements produced by stimulation of the quadrigeminal bodies are movements of expression. These are considered by Ferrier to be of reflex nature, and dependent on propagation of the irritation from the sensory centres, to the motor centres and nerve-fibres.

The leading function of the quadrigeminal bodies undoubtedly is to preside over the visual impressions; and they also appear to establish various relations between these and other sensory impressions. Still we find these bodies largely developed in

the mole, in which vision is completely absent, and the sensory root of the trifacial nerve, which is very large in this animal, takes origin from the anterior tubercle.

Value of Viossens (volum medullare superius).—The only peculiarity definitely known about this structure is the decussation of the fibres of origin of the nervus patheticus, which takes place in its interior.

Cerebellum.

Structure.—As in the cerebrum, the cortical substance of the cerebellum is grey, while white matter is found in the interior. The cortical substance presents a definite structure, and is divisible into three layers: (1) the external layer, which contains (imbedded in the neuroglia) a considerable number of small angular nerve-cells, which give off fine branching processes, the connection of which have not been clearly defined. (2) A middle layer, which contains the peculiar *cells of Purkinje*, which somewhat resemble the motor cells of the cortex cerebri; they are large in size, somewhat pyriform in shape, with their apices towards the surface, and usually placed so as to form a single layer. They present two kinds of processes: (a) an axis-cylinder process, single and unbranched, which comes off from the deeper end of the cell, passes into the third layer, and probably forms the axis-cylinder of a medullated fibre; and several (3-5) protoplasm processes, which pass from the pointed end of the cell towards the surface and ramify in the first layer, forming a delicate meshwork, analogous to Gerlach's nerveplexus in the spinal cord. These cells are probably motor in function; the centripetal fibres are believed to communicate with them through the intervention of the nerve-network formed by the external processes, while the centrifugal fibres are the direct continuation of the axis-cylinder processes. (3) The third layer—the *granular* (Klein's *fibrillar layer*), contains small roundish cells, thickly studded throughout the neuroglia, and which seem to be unconnected with the surrounding fibres.

In addition to the cortical part of the cerebellum, grey matter is found in some other situations: (a) in the *corpus dentatum* (*corps rhomboidal*), which is placed in the trunk of the *arbor vitæ*, and to the inner side of its middle; (b) in the *nucleus of Stilling*, which is placed below and inside the corpus den-

tatum ; (c) in the *external auditory nucleus*, which is placed in the inner part of the inferior cerebellar peduncle, and is connected with Stilling's nucleus by commissural fibres.

The *white substances* of the cerebellum is connected with the adjacent parts of the nervous axis by three pairs of peduncles : superior, middle, and inferior. These do not require any description here.

Functions.—*Stimulation* of the cerebellum produces no evidence of pain ; motorial phenomena are the only ones produced. *Removal* of a part gives the same results as removal of the whole.

Motor functions.—The cerebellum may be considered as the centre of equilibration and co-ordination of general movements (of progression, station, flying, &c.), and is also concerned in some special movements—such as prehension of food, movements of the head, of the eye-balls, &c. According to this view, based on the results of the latest experiments, it forms a medium of connection between sensory and motorial functions, and establishes between them the relations necessary to give to the various movements the proper co-ordination and precision.

Mechanical irritation has not given constant results. Nothnagel, by pricking with a needle, has produced rotation of the head to the opposite side, curvature of the spine in the same direction, elevation of the anterior limb on the same side, movements of the tongue, of the lower jaw, contractions of the muscles of the face (including the orbicularis palpebrarum), &c. Ferrier, in experimenting on the brains of monkeys, found stimulation of the anterior part of the median lobe cause retraction of the head ; stimulation of the posterior part of the vermis causes the head to be thrown forward, and, at the same time, movements of the limbs of the corresponding side take place.

Removal of the cerebellum has given more definite results. Flourens, experimenting on pigeons, found complete ataxia to follow its extirpation. Voluntary movements are not abolished, but they are made in an uncertain and disorderly manner ; the animal is trembling and restless, but is unable to walk or to fly. According to Ferrier, these disorders are more marked when the cerebellar lesions are non-symmetrical, and are comparatively slight when corresponding parts of the lateral lobes are engaged, or when the organ is divided in the median line. Loss of co-ordinating power is undoubtedly the most prominent

result of lesions of the cerebellum. In man, pathological changes have been observed to cause peculiarities of movement closely resembling those of a drunken man (Hughlings Jackson).

From the resulting symptoms of lesion, Flourens supposed the cerebellum to be the seat of *muscular co-ordination*, while Lussana has supposed it to be the seat of *muscular sense*, to the loss of which he attributes the resulting motorial disorders. It was supposed by Gall to be the seat of *philo-progenitiveness*, but this theory, which has no physiological argument in its favor, is now mentioned only as an interesting historical fact.

Influence on the movements of the eye-ball.—Ferrier found stimulation of the lateral lobe of the cerebellum in monkeys cause deviation of both eyes to that side; irritation applied to the median lobe causes, when to the anterior part of the vermis, turning upwards of the eye-balls; when to the posterior part, the eyes were turned downwards. Contractions of the pupils is caused by stimulation of the cerebellum; it is more marked on the affected side. Hitzig has experimented on man with the galvanic current. Placing the poles of a battery in the mastoid fossæ behind the ears, the passage of the current causes a sensation of vertigo, the head and the eye-balls are turned to the positive pole, and external objects, at the same time, seem to turn in the opposite direction. If the eyes are closed the individual feels drawn towards the negative pole. Ferrier supposes that irritation of the cerebellum, in this experiment, is only at the positive pole.

Willis believed that the cerebellum influenced the movements of organic life, but this idea has not been substantiated. One such symptom, that of vomiting, has been observed in some cases of stimulation, and in pathological lesions in man.

Other functions ascribed to the cerebellum.—Some authorities (Pourfour du Petit, Foville) have looked upon the cerebellum as a centre of general sensibility (*sensorium commune*); but there is no sufficient argument in favor of this theory. It has also been supposed to form an *instinctive* or *intellectual centre*. The hypothesis of Gall has been already referred to, but is generally disbelieved. It has, however, been adopted of late years by Lussana, who placed there both the *muscular sense* and the *erotic sense*.

Cerebellar peduncles.—Lesions of the cerebellar peduncles vary according to the peduncle engaged, and the extent of the

lesion. The results are partly confounded with those of lesion of the cerebellum itself. Section of the middle peduncle causes rotation around the axis of the body; if the injury is at the posterior part, the rotation is to the side affected (Magendie); it is on the side opposite to the lesion when the anterior part is engaged (Schiff, Claude Bernard). Injury of an inferior peduncle causes pleurosthotonos on the affected side (Rolando, Magendie); the curve is in the opposite direction when the lesion affects a superior peduncle.

Movements of rotation.—Four varieties of rotatory movements have been observed in connection with lesions of the encephalon. Their production cannot be explained in the present state of our knowledge. (1) *Circus movement.*—In this form the animal describes a circle of greater or less diameter by moving around the circumference in a direction, either similar, or opposite, to that of the movement of the hands of a clock. In some cases, instead of continually moving in the same circle, it describes curves of varying radius, forming a kind of spiral. This movement has been chiefly observed after lesions of the crus cerebri, but it has also been observed in a case of lesion of the cortex. (2) *Rotation in the arc of a circle.*—In this movement the animal turns round its posterior extremity, which forms the centre of a circle, of which the body forms the radius, while the head describes the circumference. This somewhat rare form of rotatory movement has been observed by Schiff and Brown-Sequard after lesions of the pons and of the anterior quadrigeminal bodies. It was seen by Beaunis after a lesion of the optic thalami. (3) *Rotation around the longitudinal axis of the body; rolling.*—This has been observed after lesions of the middle cerebellar peduncles, and also in case of injury of the upper and outer part of the cerebral peduncles. The direction of the rolling is determined by the side on which the animal happens to fall. (4) After removal of the nucleus caudatus in one case, a circular movement was observed, in which the feet of the sound side described a circle, while those of the paralysed side formed a pivot.

Cerebrum.

Structure of the cortex cerebri.—Meynert has divided the cortex microscopically into five layers: (1) most externally is a *hyaline layer*, consisting almost entirely of neuroglia, with a few small angular cells scattered about in its substance; (2) a layer thickly studded with small pyramidal cells, with the apices towards the surface; (3) the deepest, in which large pyramidal cells (*motor cells*) are similarly placed, but not so closely set; (4) a *granular layer* containing numbers of small irregular cells; (5) a layer of elongated, fusiform cells of considerable size

(*cellules volumineuses de la volition* of Robin), the long axis of which are placed parallel to the surface. The pyramidal cells of the third layer were first described by Betz in the *lobulus paracentralis*; the angles send off branching processes, while a single, undivided, axis-cylinder process comes off from the centre of the base, and, according to Meynert, becomes continuous with the axis-cylinder of a motor nerve fibre.

The *medullary* (white) substance of the cerebral hemispheres presents a structure similar to that of the white substance of the spinal cord.

Notwithstanding the numerous experimental and pathological observations which have been collected on the subject, the functions of the cerebral hemispheres have not been by any means clearly defined. After removal of the hemispheres in the frog, it retains its power of preserving the normal attitudes, but remains immobile except when provoked by external stimulation; when thrown into water, it swims about with perfectly co-ordinated movements, and, when placed on the back, it turns. It possesses the power of maintaining its equilibrium, and if the skin of the back be lightly stroked between the shoulders it croaks, and the croaking is repeated so long as this stimulus is continued (Paton, Goltz). In pigeons, removal of the cerebrum throws the birds into a soporific state, from which, however, they can be roused by irritation, which causes them to open their eyes and shake their wings; then, after a little movement, they again fall into the state of sopor. When pushed they walk; thrown into the air they fly; sensation and motion seem to be preserved; perception and volition are lost. They live a considerable time if taken care of, and even some amount of regeneration of the nerve-tissue takes place (Voit). In mammals, similar phenomena have been observed, but death rapidly supervenes.

Localisation of cerebral functions.—Two hypotheses are maintained about the functions of the hemispheres. (a) Some high authorities (Flourens, Brown-Sequard, Goltz, &c.) deny the existence of distinct seats for the different functions or perceptions. When one faculty is destroyed, all disappear. The nerve-cells of the cerebrum all have the same functions, according to Brown-Sequard, and cases of extensive cortical lesions, without any failure of intelligence, are quoted in favour of this view. (b) Other observers (Hitzig, Ferrier, Charcot) believe that the

functions of voluntary motion and conscious sensibility have definite seats in the cortex cerebri.

Motor centres.—In favor of the existence of definite motor centres in the cortex cerebri, the following arguments are used by those who believe in their existence. (1) *Stimulation* of certain parts of the surface of the hemispheres causes contractions of definite groups of muscles. The *motor zone* is placed in the region of the fissure of Rolando, while the *latent zone*, which causes no movements when stimulated, occupies the greater part of the surface. Against this theory it has been objected, that the stimulants applied to the cortex are transmitted to the white fibres beneath; while Schiff believes that the movements so obtained are merely reflex in their nature. It has also been objected that the results of stimulation are so variable, and so differently reported by different observers, that no deductions can be made from them. (2) *Destruction* of a motor centre destroys the power of the movements which were provoked by stimulation of that centre. But Schiff will have it that the motorial disorders which result in these cases, are due to the loss of tactile sensibility, and the consequent ataxia; while Nothnagel, and Hitzig himself, refer them to loss of muscular sense. Tripier has, however, shown that section of the posterior nerve-roots (which contain the sensory nerves of muscle), or section of the cutaneous nerves, will not cause similar disorders of motion. There is, however, one very forcible objection to the theory: it is, that the paralysis produced by ablation of the motor centres is always temporary and disappears completely in a short time. Still, this may be due to the motor functions being supplied in one of the following ways: (a) by increased activity of the corresponding centre on the opposite side; this explanation, however, will not suffice, as bilateral destruction of a motor centre does not prevent the return of motor power, nor does section of the corpus callosum (Carville and Duret); (b) that the adjacent parts of the cortical substance take on a vicarious action forming new motor centres (this idea is advocated by Carville and Duret); (c) the inferior centres (in corpus striatum, &c.) may take on increased action and supply the requisite function (Luciani, &c.); (d) Francois-Franck has supposed that an explanation might be found in the hypercinesia of the spinal centres, which are maintained in a state of activity by the centres of the opposite side; but there is

the same objection to this idea as to the first mentioned. Still this return of active movements, although the strongest objection to the localisation theory, is not an unvarying result; and, according to Ferrier, it does not take place in the monkey, or in man, in whom automatic movements are less easily established than in the dog. He explains the return of movement by the increased activity of the inferior centres.

(3) The records of clinical facts are in favor of the existence of localised motor centres. Most of the evidence in this line has been collected by Charcot and his pupils. Destruction of the motor areas by disease has been followed by the corresponding local paralyses (*monoplegia*), while pathological changes in any part of the so-called *latent zone* give no result. Irritation by tumors, &c., of the motor zones, causes corresponding muscular spasms, while atrophy of these centres has been seen to exist in cases of congenital malformations, and after amputation. Disease or extirpation of a part of the motor zone, is followed by descending degeneration of the fibres leading from that part; and the path of degeneration may be traced down the cord.

(4) The motor cells of Betz have been found only in the motor zone, and according to Lewis and Clarke they are accumulated in the parts which correspond to Ferrier's motor centres.

Motor centres in man.—The localisation of the motor centres in the human cerebrum, is still in a state of considerable uncertainty. Those which have been defined by various observers are the following :—

(1) *The centre of articulate language.*—This was formerly placed by Bouillaud in the anterior lobe, and has since his time been more definitely located, by Broca and his followers, in the posterior third of the inferior frontal convolution of the left side. It does not appear to be a single centre, but several neighboring ones seem to be engaged in the function; for some lesions of this convolution are followed by loss of memory of words; some by loss of the signs which represent them; some by ataxia of the muscles concerned in the production of speech, or in the writing of the words which it is required to express. These several results may be taken as presumptive evidence of the existence of the centres of which they express the lesions.

(2) *Centre of movements of the lower part of the face.*—This is placed a little above the last; Charcot and Pitres place it in

the lower part of the two convolutions which limit the fissure of Rolando.

(3) *Centre for movements of the upper limb.*—This is placed by Charcot and Ferrier high up on the margins of the fissure of Rolando, engaging both its anterior and posterior borders.

(4) *Centre for movements of the lower limb.*—This is situated above the last. According to Charcot it occupies the *lobulus paracentralis*, the superior third of the ascending frontal convolution, and the two superior thirds of the ascending parietal.

(5) *Centre for movements of the head and neck.*—The situation of this centre is not yet definitely settled; it is probably near the posterior end of the second frontal convolution.

(6) *Centre for movements of the eyes.*—According to Ferrier this centre is joined with the last mentioned.

Sensory centres.—(1) *Visual centre.*—In the monkey, Ferrier has found this centre to correspond with the region of the *pli courbe*. Destruction of this region causes blindness (*amaurosis*) of the opposite eye, which, however, disappears after some time, but if the lesion be bilateral, the blindness is permanent. In man's brain Wernicke has recorded a case of hemiopia dependant on softening of a patch of cortical substance on the convexity of the occipital lobe; also unilateral blindness has been known to follow embolism of the posterior cerebral artery (Bastian). Atrophy of the region of the visual centre was found by Munk to exist in case of an infant of a few months old, from which one eye had been removed after birth.

(2) *Auditory centre.*—This centre has been placed (in the monkey) at the superior part of the temporo-sphenoidal convolution by Ferrier and Luciani; but Munk places it a little lower down. Destruction of this part of the cortex causes temporary deafness on the opposite side, but bilateral destruction is followed by permanent deafness (*cophosis*).

(3) *Olfactory and gustatory centres.*—Ferrier places these centres in the upper part of the temporo-sphenoidal lobe, while H. Munk believes it to be in the gyrus hippocampi, which indeed was always affected in the lesion produced by Ferrier's experiments.

(4) Ferrier is disposed to place the centres of tactile sensation and general sensibility in the hippocampal region, but this location has been questioned by Munk and others.

Centres of organic functions.—(1) *Thermic centres.*—In the region which corresponds in the dog to the motor centres of the hind limbs, and the flexion and rotation movements of the fore limbs, it has been found that increase of temperature follows destruction of a certain part, while stimulation causes chilling of the opposite limbs (Eulenburg, Landois, Hitzig). This, however, has been contradicted by Kuessner.

(2) *Vaso-motor centres.*—The existence of these centres in the cortex cerebri, although denied by many, is asserted by some high authorities. Lepine has seen stimulation of the post-frontal gyrus produce increase of the vascular pressure in the limbs of the opposite side. Bacchi and Bochefontaine have found electric stimulation of the anterior part of the crucial sulcus and of the olfactory lobe produce constriction of the retinal vessels of both sides. Balogh has found five points on the surface of the brain, the stimulation of which influences the rate of the heart's action, and Bochefontaine found four points of which the stimulation increased the blood pressure, and three points which diminished it. Electrification of the brain in the rabbit has been followed by pulmonary hæmorrhages (Heitzler); and articular hæmorrhages in the dog have been produced by stimulation of the sigmoid gyrus (Albertoni).

Psychical centres.—Ferrier and many other physiologists have endeavoured to localise some of the intellectual functions. They would place *attention, reflection, concentration of thought* (indeed *intellectual activity* properly so called) in the anterior part of the frontal lobes. Other authorities, such as Flourens, Brown-Sequard, Goltz, Munk, believe that reason and intelligence have no special seats in the cortical substance of the brain.

Centres of emotion.—Ferrier, basing his hypothesis on the localisation of visceral sensations in the occipital lobe, places the seat of painful and of agreeable sensations in this part of the brain; but the evidence is not sufficient as yet to establish this idea.

Centres of inhibition.—There is no doubt that the brain exercises an inhibitory influence on the spinal centres, as is shown by the effects of section of the cord. It is also shown by the effect of directing the attention to actions which, as ordinarily performed, are of the semi-involuntary or reflex

type; such as breathing, swallowing, walking, &c., and observing the irregularity which results.

Duality of the Cerebral Hemispheres.—The hemispheres appear to be usually symmetrical, or nearly so, in function as well as in structure. The left hemisphere is found, on careful examination, however, to be usually the larger of the two, as it is also the more rapid in growth. It is known to have the possession of the centre of articulate language, and Luys attributes to it other acquired functions, such as writing, music, &c. *Alternation* of the activity of the hemispheres has been observed by Gellé and Charcot in hysterical patients. If in a case of hysterical hemianæsthesia, the sensibility be restored at one point (by metallotherapy, electricity, &c.) it is found that sensibility is lost on the symmetrical part of the opposite side. If the sensibility of two symmetrical points of the skin be explored by the æsthesiometer, and a sinapism is applied on one side, the sensibility is found to be increased on that side, and diminished on the other to a corresponding extent. Curious phenomena of the transfer of visual sensations in hysterical and hypnotic subjects have been observed by Charcot, Landolt, &c.

Cerebral thermometry.—In ordinary conditions the temperature of the brain is higher than that of arterial blood (R. Heidenhain). Careful researches on the subject have been made by Broca, Lombard, and others, by external examination of the temperature of the head. They have found that of the left side somewhat higher than on the right, while the anterior region is warmer than the posterior. It is higher in man than in woman, in the infant and youth than in the adult. The temperature is elevated by mental work; and the increase is more on the anterior region and right side than in the opposite directions. According to the researches of Schiff, this increase of temperature is independent of the circulation, and is also seen to follow tactile, visual, or auditory stimulation, or functional activity. The results of external thermometry must, however, be applied with caution to the cerebral temperature; as, according to François-Franck's observations, an increase of three degrees of the temperature of the brain produces an external elevation of only one-tenth of a degree.

Influence of Cerebral Activity on the Various Functions.—Mental work increases the bulk of the brain, as has

been observed in individuals, after the operation of trepanning Mosso, François-Franck, &c.), and the increase would seem to be due to activity of the circulation ; but François-Frank is disposed to refer it to the modification of the respiratory movements, which become shallower. Mosso, however, affirms that it is independent of the respiratory rhythm. The influence of the cerebral activity on the pulse has been already mentioned.

The influence of cerebral activity (especially emotional), on the secretions, on muscular movements, &c., are referred to in other parts of this work.

The products of *disassimilation* of brain substance are but imperfectly known. According to Haughton and Byasson, an increase of *urea* results from active mental work. An increase of the *urinary phosphates* appears to be a constant result of cerebral activity (Paton, and others). Flint regards *cholesterin* as the most characteristic product.

Cerebral Circulation.—This has an intimate connection with that of the thyroid body, which may be looked upon as a diverticulum for the encephalic circulation. Every increase of pressure in the cerebral vessels causes slowing of the respiration and of the heart's action ; and, if the pressure becomes too great, dyspnoea, loss of consciousness and paralysis result. Compression of the brain gives similar results. Cerebral anæmia (ligature of the arteries, gyration) causes convulsions, rapidly followed by death. Cerebral congestion acts much more slowly.

Movements of the Brain.—These correspond, the larger to the respiratory movements, and the smaller to the ventricular contractions ; so that the tracings of the cerebral movements are somewhat similar to those of the arterial pressure. As the walls of the cranial cavity are inextensible, these movements require a disposition of parts which allow variations in volume, and this is afforded by the sub-arachnoid spaces, and the contained fluid (*liquor Cotunnii*, *liquor Magendie*). These spaces communicate with the sub-arachnoid spaces of the spinal cord, and, in this way, when the quantity of intra-cranial blood increases, a corresponding portion of fluid escapes into the rachidian cavity, which easily accommodates it. The volume of the brain increases greatly during exertion.

PHYSIOLOGICAL PSYCHOLOGY.

All psychical manifestations result from the activity of the brain substance. The exact nature of the processes which take place during mental activity is entirely unknown. It was believed by some of the older physiologists that thought was *secreted* by the brain substance, as the parotid gland secretes saliva, or the liver bile. As Herzen well remarks, every psychical act requires a certain time for its accomplishment; it takes place evidently in a resisting medium, and is probably a form of movement.

Cerebral activity may be conscious or unconscious, but the division is not at all clearly defined. Many mental acts, originally accompanied by consciousness, become unconscious by habit; or when overshadowed by the greater intensity of other acts performed at the same time. At any given moment of cerebral activity we have a great number of thoughts, ideas, and recollections; some of which are so prominent and important as to make vivid impressions, while others pass off without leaving any lasting traces. In speaking or in writing we neglect the intermediate ideas which pass between the formation of the initial idea and the formation of the verbal or written sign which represents it. This *unconscious cerebration*, recognized long ago by philosophers (*insensible perception* of Leibnitz, *latent consciousness* of Hamilton), plays the most important part in psychology, and embraces the greater part of the mental processes which are constantly going on within us. There is, also, no doubt that these unconscious sensations form the stimuli which give rise to the forms of cerebral activity, which results in movements, ideas, and determinations of which we are conscious.

Herzen refers consciousness to disintegration of the nervous elements; while its absence corresponds to the periods of unconsciousness, sleep, &c. By means of this hypothesis, he endeavors to reconcile the opposed theories of Lewes and Maudsley, the former of whom supposes the omnipresence of consciousness in every nervous central act, including even the simplest spinal reflex; while the latter makes consciousness to be merely a kind of epiphenomenon of mental activity.

Two theories have been advanced for the explanation of the phenomena of consciousness: (1) That which is more gene-

rally admitted makes the centres of consciousness to be distinct from the other centres. Being connected with the sensory centres by commissural fibres, a part of the stimulus which is conveyed to a sensory centre travels upwards to the centre of consciousness, while the other part is reflected along the efferent nerve to the muscle, &c. Prolonged repetition of the stimulus has the effect of determining the course of the impulse along the efferent nerve, to the gradual exclusion of the other path, so that in time an act originally conscious becomes automatic or mechanical. (2) According to the other hypothesis, all nervous acts are originally conscious, and gradually become unconscious by habit.

Intensity of Sensations.—This depends on two conditions: (1) intensity of the stimulus, and (2) the excitability of the sensory organ. Still it is found that, with equal irritability, the intensity of the sensation does not increase in proportion to that of the stimulus applied. Careful investigations of this subject have enabled Fechner to formulate the following *psycho-physical law*: *the sensation increases as the logarithm of the stimulus*. This law presents certain limits: below a certain intensity of stimulus no sensation is produced; this minimum stimulus is the limit of excitation (*Reizschwelle*). Beyond the upper limit of excitation, all sensation is changed to pain; this superior limit is called the maximum of excitation. Between these limits the law of Fechner has been approximately verified: that is to say, when the stimulus follows a geometrical progression, 1, 2, 4, 8, &c., the resulting sensation increases in arithmetical progression, 1, 2, 3, 4, &c.

Elaborate experiments on the subject have given the following *minima* of stimulation necessary to produce various sensations:—

Tactile sensations: pressure of .002—.05 gramme;

Sensations of temperature: .125° C. (.257 F.); the skin being at a temperature of 18°.4 C. (65°.12 F.);

Auditory sensations: a ball of 1 mgr. in weight, falling through a height of 1 mm. at a distance of 91 mm. from the ear;

Muscular sensations: shortening of the rectus oculi internus by 1 mm.

Visual sensations: light, $\frac{1}{3}$ that of the full-moon, or the lighting of a dark screen by a wax candle placed at a distance of .513 metre. According to the preceding rules the

following formula gives the value of a sensation (S) in terms of the intensity of the stimulus (r), the perceptible minimum (g), and a constant quantity K : $S = K \log. \frac{r}{g}$. Delboeuf has formulated a law differing somewhat from that of Fechner, by recognising the influence of the *fatigue element*, which was ignored by Fechner. Fechner's law has been vigorously attacked by Hering and some other physiologists.

EXTERIORITY AND PROJECTION OF SENSATIONS.

According as sensations are referred to our own bodies or to the outer world, they are spoken of as *subjective* or *objective*. Some subjective sensations are referred to the surface of the body, such as the tactile and gustatory; while others are referred to the interior of the organism (hunger, thirst, &c.). The objective sensations are those of sight and hearing, which are referred to the outer world, by a process of projection which is obviously a psychical act of reasoning, and is developed by habit. With regard to hearing, it is often difficult to separate the so-called *entotic* sounds from those produced externally. The psychical acts on which the projection of auditory and visual sensations depend are, in a great measure, dependent on muscular sense; objects seen and heard are mentally referred to a distance when we learn how far we have to displace our hands to seize them. They are probably referred to the immediate vicinity of the body in early infancy.

For an understanding of the nature of our sensations, it is necessary to remember that we do not really know external objects; we know but the states of consciousness produced by them. Our perceptions are not the images of objects, but the action of objects on our organs; all our sensations are primarily subjective, and such they, in all probability, were in the early days of extra-uterine existence. From that time the gradual mental training produced by experience had the effect of transforming rough sensations into perceptions, of creating the necessary distinction between the internal and the external world, between the *EGO* and the *NON-EGO*.

LANGUAGE.

Language may be divided into *emotional* and *rational*. The former is more highly developed in the lower animals, and in

man during infancy and savage life. The latter is characteristic of man, and, according to Max Müller, Romanes, and some others, is the great distinctive attribute of *homo sapiens*. "The point where the animal ends and man begins," says Max Müller, "can be determined with the greatest precision, for it coincides with the period of commencement of language." Two conditions are necessary to the production of articulate language: (a) a certain degree of intellectual development, and (b) a cerebral organ of articulate language. But observation of the communications of the lower animals is quite enough to show that a kind of rudimentary language is used by many species, which surpasses the limits of emotional ejaculations, although, perhaps, not attaining the standard of Max Müller's rational language.

VOLITION.

The difference between voluntary and involuntary acts consists in this particular: we have consciousness of the involuntary act only when it is accomplished, while the idea of the voluntary act pre-exists in the mind before it is done. In case then of a voluntary act called forth by a sensation, there are three successive acts which correspond to the successive stimulation of three centres: (a) a sensory centre by the stimulus conveyed along an afferent nerve, (b) an intermediate centre of consciousness, which transmits the stimulus to (c) the motor centre, from which it passes along the efferent nerve to the muscle or muscles whose action is necessary for the performance of the required movements.

The question of *free-will* in action is one which is entirely beyond the reach of exact science, and must be answered by each individual for himself. It is well, however, to remember that a great part of the psychical acts of our mind entirely escape our notice, and that many of our apparently free resolves are but the resultant of our native structural and mental peculiarities, our early education and surroundings, and the sensations or emotions passing unconsciously through the mind at the same time.

RAPIDITY OF PSYCHICAL PROCESSES.

The duration of sensory perceptions has been calculated with great care by Exner from numerous observations on dif-

ferent individuals. The durations of the following require to be taken into account in making the calculation :—

- (1) Of the latent period of stimulation of the sensory apparatus ;
- (2) Of the passage of the stimulus from the sensory surface to the nerve-centre ;
- (3) Of the sensory transmission in the spinal cord ;
- (4) Of cerebral transmission and the cerebral acts ;
- (5) Of the motor transmission in the cord ;
- (6) Of the motor transmission from the cord to the muscle ;
- (7) Of the latest period of stimulation of the muscle.

(2) and (4) are known ; the velocity of a sensory stimulus being about 30—35, and of a motor about 33 metres per second. (3) has been calculated to occupy about .1749 of a second for stimuli coming from the foot, and .1283 for the hand ; this gives a rate of about eight metres per second. (5) is about .1506 sec. for the foot, and .184 for the hand, which gives a rate of eleven or twelve metres per second. (1) lasts but a very short time ; for visual sensations about .02—.04 sec.

The *duration of sensory perception* (4), is calculated by deducting from the total process the sum of 1, 2, 3, 5, 6, and 7. The following are the periods obtained by Exner, with the ages of the individuals : .2053 sec. (20 years) ; .0775 (22) ; .2821 (23) ; .1231 (24) ; .0828 (26) ; .0901 (35) ; .9426 and .3350 (76). These variations in different individuals had long been familiar to astronomers, and special allowances made for the time that elapses between the passage of a star before the field of the telescope and the appreciation of the event by the observer. This varying period is called the *personal error or personal equation*, and although constant for the individual it may be gradually diminished by exercise (Wolff). Fatigue tends to increase the duration of all psychical acts, while it is diminished by attention.

Donders has invented for the measurement of the duration of psychical acts two instruments, of which one, the *nematochometer*, calculates the time required for a simple idea ; the other, *nematachograph*, is for the purpose of determining the duration of more complex ideas.

SLEEP.

During life the cranial nerve-centres present the two condi-

tions of sleep and wakefulness (rest and activity), the alternation of which is absolutely essential for existence. The real cause of sleep is still undetermined ; none of the theories which have been offered will satisfactorily account for its phenomena. To say that it is a state of nervous repose is no explanation. Preyer considers it analogous to muscular fatigue, and attributes its onset to the action of the products of metamorphosis of nerve-tissue, especially lactic acid, but this idea is purely hypothetical. It has been attributed by Sommer and some other physiologists to a diminution of oxygen ; and, indeed, Pflüger, by depriving frogs of oxygen, has thrown them into a kind of sleep, or apparent death. Again, other authorities try to reconcile these theories, admitting the diminution of oxygen during sleep, and suggesting that the oxygen present was used up in the consumption of oxidising the fatiguing (*ponogenic*) substances which had accumulated in the brain during the hours of wakefulness.

When sleep is profound all the phenomena of psychical activity appear to be suspended, and the condition, from a functional point of view, resembles that of an animal whose cerebral hemispheres had been removed ; the functions of nutrition, digestion, respiration, circulation, &c., still continue ; sensory stimuli are followed by movements of a purely reflex nature, and, in short, the cessation of the functional activity of the cerebral hemispheres may be compared to what occurs in a secreting gland. This state of profound sleep is usually observed but in the early moments ; it gradually becomes lighter, and the cerebral centres take on some degree of activity, as is shown by the phenomena of dreams, and by the remarkable feats of memory which are sometimes performed. As a great part of the dreams, ideas, and words of the sleeper undoubtedly pass without recollection, it is impossible to say whether the cerebral repose is absolute at any moment of sleep. Mosso, in the course of the experiments already alluded to, found that pronouncing the name of the sleeper caused a modification of the volume-curve of the cerebral mass, without awaking him, or leaving any remembrance in his mind.

The want of sleep is felt by a series of sensations familiar to everyone ; muscular sensations connected with the upper eye-lid and infra-hyoid muscles leading to winking and nodding ; heaviness of the limbs and of the head ; diminution of

muscular and tactile sensibility, &c. During sleep the action of the heart and the respiratory movements become slower, the latter being almost entirely thoracic (Mosso). All secretions are diminished, also the elimination of carbonic acid. The eye-balls are rotated upwards and inwards, the cornea is dry, and the pupils contracted. The state of the cerebral circulation is still disputed, but the majority of observers incline to the idea that anæmia prevails. It has been maintained by Durham, Hammond, Ehrmann, &c., and is borne out by the experiments of Mosso, Franck, and others. Some, however, assert that congestion exists, arguing from the congestion of the conjunctiva and contraction of the pupil, which would indicate vaso-motor paralysis.

CHAPTER XI.

DIGESTION.

THE great bulk of the aliment which is introduced into the stomach is in a condition entirely unfit for absorption ; and before contributing, in any way, to the nutriment of the body, must be subjected to the action of certain fluids, which modify it in such a manner that a large proportion easily passes into the blood, either directly through the capillary walls, or indirectly through the lacteals. The smaller part passes away from the bowels.

The various steps of the digestive process were divided by Magendie into eight stages : (1) prehension ; (2) mastication ; (3) insalivation ; (4) deglutition ; (5) chymification ; (6) chyli-fication ; (7) absorption ; (8) defæcation.

The first stage, which consists in seizing the morsel and placing it within the mouth, though very essential, requires no special description in a work on physiology. It is performed in man by the hands, lips, tongue, and incisor teeth.

Before examining the physiological functions of the different digestive organs, we shall examine the structures of each in their order.

Teeth.—Three essentially distinct parts enter into the formation of a tooth : *dentine*, *enamel*, and *crusta petrosa*.

(a) *Dentine* or ivory (*osteodentin*), makes up the great part of the body of a tooth. It presents, on microscopic examination, (1) a densely hard, homogeneous ground substance, made up of lime salts (like those of bone), imbedded in a reticular matrix ; (2) minute canals, passing spirally from the pulp cavity to the surface, in a direction perpendicular to the latter. They become finer as they pass out, and communicate by delicate lateral branches. Each is lined by an elastic membrane (*dentinal sheath of Neumann*), which resists the action of acids and alkalis. (3) Each dentinal canal contains a *dentinal fibre* of Tomes ; these are processes of columnar nucleated cells, which form a single layer lining the pulp-cavity (*odontoblasts* of Waldeyer).

When traced to the surface of the dentine, the canals are found to open into the *interglobular spaces* of Czermak. The *interglobular substance* (*granular layer* of Purkinje and Tomes) which contains these spaces, is but the superficial, imperfectly calcified layer of dentin; it forms a series of distinct layers (*incremental lines* of Goltz). The adjacent surface of the dentine present rounded elevations (*dentin spheroids*). Parallel to the surface are the *lines of Schreger*, which are due to "the optical effect of simultaneous curvatures of the dentinal fibres" (Klein). The interglobular spaces are cavities of varying size, communicating with one another by very fine canals, and containing nucleated protoplasmic corpuscles, the branches of which communicate with one another and with the dentinal fibres. According to some authorities (Kölliker, Tomes, &c.) the dentinal fibres also pass into the enamel.

(b) Enamel (*substantia adamantina*) covers the crown of the tooth. It is formed of closely-set hexagonal prismatic rods (*enamel prisma*), placed vertical to the surface, and arranged in bundles which cross one another. Horizontal curved lines running nearly parallel to one another are also seen (*contour lines* of Owen, *parallel brown stripes* of Retzius). The adjacent enamel prisms are united by a very thin layer of interstitial cementing substance, and the surface is covered with a layer of non-nucleated horny scales (*enamel cuticle* of Kölliker, *perident capsule* of Nasmyth).

The *cement* (*crusta petrosa*) is composed of imperfectly lamellated osseous substance. The lacunæ and their contained osseous corpuscles are exceptionally large, and the canaliculi very numerous. The layer of cement becomes thick as we approach the apex of the root.

The socket of the tooth is lined by a process of periosteum (*periodontal membrane*), and from this a process is sent through a hole in the fang into the so-called *pulp-cavity* in the interior of the tooth, and is continuous there with the pulp tissue. This contains blood-vessels and nerves, and is rich in nucleated branched corpuscles. The peripheral cells form two distinct layers; the outer (next the dentine surface) forms a single layer of columnar cells (*odontoblasts* of Waldeyer), which send processes into the dentinal canals, as already mentioned. Beneath the layer of odontoblasts is a layer of spindle-shaped or pyri-form cells, wedged in between the ends of the odontoblasts.

They send off processes which communicate with the cells of the matrix, and, according to Klein, processes of these cells, and not of the odontoblasts, form the so-called dentinal fibres. Nerve-fibres have also been traced between the odontoblasts, and it has been surmised, though not as yet proved, that filaments pass into the dentinal canals.

Development of teeth.—The first rudiment (*primary enamel organ*) is formed by a prolongation of the stratified superficial epithelium into the substance of the mucosa of the lower jaw, when this tissue was represented by embryonic connective tissue. The primary enamel organ becomes invaginated at its deep end by a papillary mass of gelatinous tissue, the *embryonal tooth papilla*. The primary enamel organ thus becomes the *secondary enamel organ* (enamel cap). The odontoblasts appear very early as a peripheral layer of cells on the papilla. They produce the dentine, and, according to Waldeyer and Boll, become elongated at their outer ends, and form the enamel matrix. The central part of the papilla remains as the pulp.

The enamel cap becomes differentiated into thin layers by the change of the middle strata of epithelial cells into a transparent *middle membrane*, from an accumulation of fluid between its cells. The *inner membrane* is formed of a layer of columnar cells, in contact with the dentine (*enamel cells, inner epithelium* of Kölliker). Outside the enamel cells is the *stratum intermedium* of Hannover, formed by one, two, or three layers of small polyhedral cells, each with a spherical nucleus. The *outer membrane (outer epithelium* of Kölliker) is formed of several layers of epithelial cells.

Of the teeth two sets appear—the temporary (*deciduous, or milk teeth*) and the *permanent*. The following formula show the number and arrangement of both.

Temporary—

	Molar.	Canine.	Incisor.	Canine.	Molar.	Total.
Upper	2	1	4	1	2 =	10
Lower	2	1	4	1	2 =	10

Permanent—

	Molar.	Bicuspid.	Canine.	Incisor.	Canine.	Bicuspid.	Molar.	Total.
Upper	3	2	1	4	1	2	3 =	16
Lower	3	2	1	4	1	2	3 =	16

The ages at which they appear are indicated in the following tables :—

	Molar.	Canine.	Incisor.	Canine.	Molar.
Temporary (in months)	24—12	18	9 7 7 9	18	12—24

Permanent (in years) :—

Molar.			Bicuspid.	Canine.	Incisor.	Canine.	Bicuspid.	Molar.		
17 to 25	12 to 13	6	10—9	11 to 12	8 7 7 8	11—12	9—10	6	12 to 13	17 to 25

Salivary Glands.

The mixed human saliva is formed by three classes of glands: (*a*) true salivary glands (parotid); (*b*) muco-salivary (submaxillary); (*c*) true mucous glands (sublingual). In addition to these larger glands, the small mucous glands about the mouth, labial, buccal, lingual, and palatine, all furnish a small proportion of the mixed human saliva.

Parotid.—If Steno's duct be traced down to its extremity, it will be found, by successive ramifications, to form numbers of minute canals which at last terminate in small bladder-like dilatations (*acini*, *alveoli*). The duct itself is lined by a layer of columnar cells, resting on a delicate basement membrane, and possesses a thick wall of dense fibrous tissue, also containing some smooth muscle cells. Its primary branches, the *lobar* ducts, possess a relatively larger lumen, but the tissues of the walls are similar. The columnar epithelial cells present a well-marked intra-cellular network, the fibres of which are chiefly longitudinal, and the nucleus is placed in the outer part. The *intralobular* ducts (*salivary tubes* of Pflüger) have a proportionally smaller lumen, and are lined by a layer of columnar cells, which present closely-set, longitudinal rods (Kölliker). These have been shown, by Klein, to possess small anastomosing lateral branchlets. The striation is generally better marked in the inner part of the cell. The basement membrane is, probably, endothelial, as it presents oval nuclei here and there (Klein).

Before passing into the gland substance these ducts present a change of structure, forming the *terminal*, or *intermediary* duct of Ebner. This is narrower than the other, and its lining epithelium is variable. In the submaxillary gland of man it is formed by a layer of flattened cells. This tube may branch before entering the gland substance. The proper gland-substance is found on section to be made up of branched tubes, presenting a convoluted and wavy appearance (Grot, quoted by Klein).

The acini are lined by a single layer of high columnar cells, each of which has a clear nucleus placed in the outer part. The lumen is small and, during secretion, is smaller, on account of the swelling of the cells. The basement membrane presents nuclei here and there, and is made up of branched and flattened cells connected with each other (Henle, Heidenhain, &c.)

During stimulation of the sympathetic (in the rabbit), the alveolar cells of the parotid are seen to diminish very much in size, while their contents become very opaque (Heidenhain).

Submaxillary; sublingual.—The differences which serve to distinguish the muco-salivary glands are found in the alveoli. The latter are larger, the lumen is more spacious, its lining cells are longer, and instead of the single layer, found in case of the parotid gland, we have two kinds: (*a*) *mucous* cells (Heidenhain), or central cells, forming a single layer, lining the acinus all around. These are high, columnar, transparent cells (some presenting the appearance of goblet cells), and having nuclei near the *membrana propria*. A transparent substance (*mucigen* of Heidenhain) fills the meshes of the intercellular network. During secretion this is changed into mucin, and, accordingly, in the active state of the gland, it is found to stain deeply with hæmatoxylin. (*b*). The *protoplasm* cells (*albuminous cells* of Asp) form a thin layer of crescentic outline (Fig. 53, *c c*) at the distal part of the acinus, between the mucous cells and the basement membrane (*crescent* or *lunula* of Gianuzzi). These parietal cells present a granular appearance, and are polyhedral in form, with a spherical nucleus (Heidenhain, Asp). During secretion they become enlarged, and stand out prominently under the basement membrane. In an exhausted gland the mucous cells are found to have disappeared, while the protoplasm cells of the *lunulæ* have increased in size. According to Heidenhain and others,

the latter then come to replace the mucous cells. The accuracy of this view has, however, been disputed, and the question is still *sub judice*. In ordinary secretion, according to Klein, the mucous cells are *not* destroyed; the transparent mucigen which filled the meshwork in the resting state is changed into mucin during activity, which absorbs water and is swollen up.

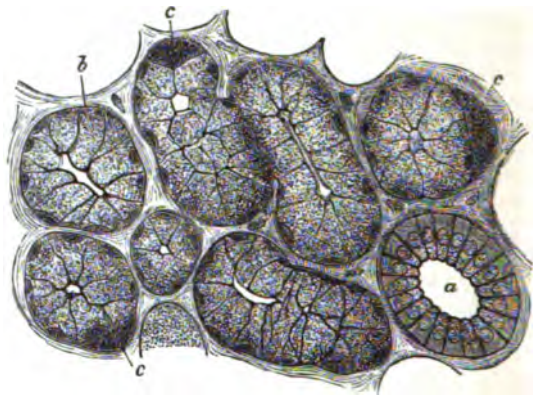


Fig. 53. Section of submaxillary gland of rabbit.

Blood-vessels are distributed to the alveoli, around which they form a dense capillary plexus, and between this and the surface of the acinus are lymph-spaces and clefts, surrounding the alveoli wholly or in part.

Medullated *nervous-fibres* from plexuses in the interlobular connective tissue, and ganglionic cells are interspersed, mostly unipolar. According to Pflüger the fibres from the plexuses pass to the epithelial cells of the alveoli, and dropping the medullary sheath, the axis-cylinder becomes continuous with the cell-substance. With regard to the salivary glands, of man and mammalia at least, the results of Pflüger are almost universally denied by other observers.

The mucous glands of the oral cavity do not present any remarkable peculiarity of structure. The largest are those of lower lip and soft palate. The duct of each gland opens on the free mucous surface with a funnel-shaped mouth, and usually in an oblique direction. The stratified epithelium of the

mucous membrane passes into the ducts for a short distance, but is soon replaced by the ordinary columnar epithelium, which, in turn, becomes flattened in the smaller branches. In the submucous tissue, the duct branches, and the divisions terminate usually in small acini, lined with large clear columnar (mucous) cells. In some situations there are small *lunule* formed by granular cells.

Œsophagus.—The Œsophagus or gullet forms a musculo-membranous tube, which reaches from the lower end of pharynx opposite the fifth (sixth, Braune) cervical vertebra to its termination in the stomach opposite the eleventh dorsal. Its course is not quite vertical, as it forms two or three slight deviations from a direct line, which are described in all the anatomical text-books. Its length averages about nine inches. Its coats are fibrous (adventitia), muscular, submucous, and mucous.

The fibrous coat is formed merely by a condensed layer of areolar tissue. The muscular coat presents an external longitudinal and an internal circular layer. The former, which is the thinner of the two, is attached above to the vertical ridge on the back of the cricoid cartilage, below which it spreads out so as to form a complete investing layer. Between this and the circular layer the plexuses of nerve fibres and ganglion cells are found, nearly similar to the corresponding structures in the rest of the alimentary canal. The circular layer, which is thicker, is separated above from the lower border of the inferior constrictor of the pharynx by the inferior laryngeal nerves and vessels, while it is continuous below with the oblique fibres of the stomach (?). The muscular fibres are striated in the upper third; they then are rapidly replaced by smooth muscle cells, which continue to the end, with a few striated fibres scattered between. The submucous coat is formed by a layer of loose connective-tissue, which allows the mucous membrane to fall into longitudinal rugæ during repose. Imbedded in it are mucous glands, of which the structure is similar to those of the buccal cavity. In the lower end they form a continuous layer for about half an inch, the *cardiac glands of Cobelli*. The ducts pass to the free surface in a horizontal or obliquely downward direction, and open with a narrow mouth on the free surface. This layer also presents, immediately beneath the mucous membrane, a longitudinal layer of smooth muscle cells (*muscularis mucosæ*), blended above by a lateral band with the

lower margin of the inferior constrictor of the pharynx. The mucous membrane is formed by dense connective tissue, with conical or cylindrical papillary projections; and lined with a stratified pavement epithelium of great thickness. The submucous tissue contains a plexus of nerves communicating with the intermuscular plexus, and containing isolated ganglion cells (Klein).

Stomach.—The stomach is covered on its anterior and posterior surfaces by peritoneum, and this membrane, which adheres closely on the surfaces, leaves considerable room at the upper and lower borders, which is necessary for the ramifications of the vessels, and to allow distension by food.

The muscular coat is made up of three layers of fibres: an external (thin) longitudinal, which is continuous with the longitudinal layer of the œsophagus; an internal (stronger) circular layer, which is continuous with the circular coat of the duodenum; an oblique layer, which is not continuous with any other fibres of the alimentary canal (Luschka). The longitudinal fibres are best marked along the curvatures, especially the lesser, and the circular are more highly developed at the orifices, especially the pylorus. The oblique fibres (first described by



Fig. 54. Muscular fibres of stomach from the inside (Luschka).

Thomas Willis, 1683) are arranged in the form shown in the adjacent figure.

Beneath the muscular fibres is the submucous coat which is formed by a loose meshwork of connective-tissue fibres. In this layer is the muscularis mucosæ, which is placed close to the extremities of the gland-tubes. In some places it consists of a single longitudinal layer, in other situations there is an outer longitudinal and inner circular layer of smooth muscle; while in a few spots there is a third oblique (or longitudinal) layer placed inside the other two. Bundles of muscular fibres pass from the muscularis mucosæ here and there, and terminate between the gland-tubes. The looseness of the submucous coat allows the mucous membrane to be thrown into longitudinal folds when the stomach is empty.

The epithelium which lines the gastric mucous membrane is formed of a single layer of columnar cells, which here and there present the characters of goblet-cells, already described. "This is especially the case during digestion, when all the cells are secreting mucus" (Klein). If the surface be examined with a lens of low magnifying power, it is found to be pitted all over with shallow polygonal depressions (the *stomach-cells* of Sprott Boyd), from the bottom of which the mouths of the gland-tubes are seen to lead off. Of these tubular glands there are two varieties: the *peptic (cardiac)* glands, and the *mucous (pyloric)*.

Peptic glands.—The peptic glands were so called because they alone were supposed to be concerned in the secretion of gastric juice. They abound in the cardiac region of the stomach, and form straight or slightly wavy tubes, two or three of which lead into a common duct, which is about a third or a sixth of the whole length; but the proportional length of the tube diminishes in the cardiac region. The tubes are generally hooked at the blind end. Each itself presents for examination a *neck, body*, and *fundus*. The neck is comparatively narrow. The epithelium of the duct is a continuation of that of the surface of the stomach, and is prolonged into the neck; where, however, the cells are very much shorter, the nucleus smaller, and the remaining substance of the cell more opaque. As the cells are traced towards the fundus, they gradually become larger again. Outside this epithelial lining is an incomplete layer of oval or spherical cells, placed immediately beneath the base-

ment membrane. They are most numerous at the neck, and more scattered towards the fundus. Their substance is more

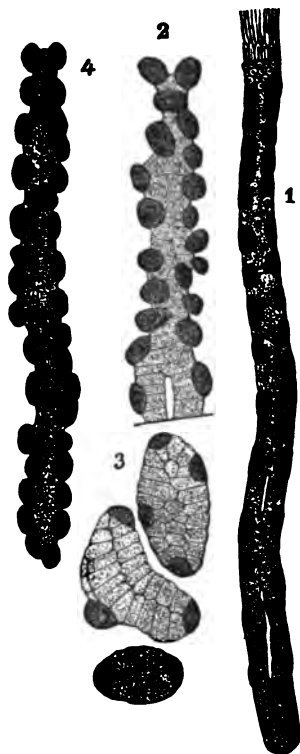


Fig. 55.
Cardiac glands (after Heidenhain).
1 shows appearance during fasting; 2, 4
during digestion; 3, terminal part divided
obliquely.

neck of the gland they become somewhat lower, while in no part is there a second layer, as in the peptic glands. During digestion, those cells become larger and less opaque, while the nucleus, spherical during rest, is compressed and close to the membrana propria.

Blood-vessels and lymphatics.—The distribution of the blood-

opaque and granular than that of the other cells. Their relation to the internal layer was first pointed out by Rollett and Heidenhain. The two layers are distinguished by Rollett as *delomorphous* and *addomorphous*, by Heidenhain as *parietal* (*Belegzellen*) and *central* (*principal*, *Hauptzellen*). The parietal cells swell out during digestion, and cause bulging of the basement membrane, and consequent irregularity of the outline of the gland. The central cells are also enlarged, so that the whole tube is broader.

Pyloric glands.—These are distinguished from the ones just described by the disproportionate length of the duct, which is as long or longer than the tube itself, and by the form of the tube, which presents a very short neck, dividing into two or three branches, each of which is wavy or convoluted. The lumen of the neck, and still more of the body, is much greater than that of the so-called peptic glands. The layer of epithelial cells is a continuation of that of the stomach surface; in the

vessels to the muscular coat is nearly similar to what we found in the oesophagus. In the submucous tissue the arrangement is more complex. The capillaries form ensheathing plexuses around the tubes, with more or less elongated meshes. A special network of capillaries forms a dense horizontal layer, just below the epithelium. The lymphatics are very numerous, and form a network close to the fundus of the gland tubes (Teichmann, Lovén), and a plexus of larger vessels in the submucous tissue. Traced towards the surface, they run a longitudinal course between the gland tubes, and near the epithelium are found to end in loops or free dilated extremities. Near the fundus of the peptic glands, and in other parts of the submucous layer, nodules of adenoid tissue, of variable size, are found.

Nerves.—These are derived from the pneumogastric and sympathetic. Between the longitudinal and circular muscular layers is found the *plexus of Auerbach (plexus myentericus)*, which includes numerous oval or angular ganglia. In the submucous tissue, and connected with the other by anastomosing branches, is the *plexus of Meissner*, which also includes ganglia of very minute size.

Small intestine.—This tube in man measures about twenty feet in length, and gradually diminishes in calibre as it passes towards its termination. Anatomists divide it into three parts: duodenum, jejunum, and ilium. The duodenum, which is about nine inches in length, ends at the crossing of the superior mesenteric artery. Of the remaining small intestine, the jejunum includes two-fifths, and the ilium three. The coats are: serous, muscular, submucous, and mucous. The serous membrane is derived from the peritoneum, and invests the tube more or less completely in different places. Beneath this is the muscular coat, which, as in the gullet, consists of an external longitudinal and an internal circular layer. Between them is placed the plexus myentericus of Auerbach, which is formed of flattened nerve-fibrils, and presents here and there angular, flattened, ganglionic enlargements. The cells are like those of the sympathetic ganglia. From Auerbach's plexus small branches come off, which form secondary plexuses of extreme delicacy for the different strata of the muscular coats, while some communicate with Meissner's submucous plexus. The latter lies in the submucous tissue, and its branches, which are more cylindrical, form fusiform or irregularly nodular enlargements at the points

of anastomosis. Its branches are distributed to the muscularis mucosæ, the blood-vessels and glands, as well as the connective tissue of the submucous coat.

The submucous coat itself is made up of a loose network formed by ordinary connective-tissue bundles, freely supplied with blood-vessels and lymphatics as well as nerves.

Glands of Brunner.—These glandular tubes are placed in the submucous coat of the first part of the duodenum. Each is a branched and convoluted tube, lined by cells, identical in appearance with those of the pyloric glands of the stomach (Schwalbe, Watney), and presenting the same changes during secretion as the latter. The duct is narrowest at its origin, the *neck*, below which the lumen of the tube becomes considerable. The only characteristic differences between a pyloric gland and one of Brunner is the greater length of the duct of the latter, and the greater number and length of its branches.

Villus.—These processes of the mucous membrane begin to appear at the latter part of the first portion of the duodenum. Each is (on an average) about one-third to one-half a line in length, and they are so closely set that ninety have been enumerated on a square line by Krause. They continue along the whole length of the small intestine, but gradually diminish in size and number.

The axis of each villus is formed by a lacteal vessel (sometimes two) which terminates near the end in an enlarged blind extremity (sometimes a loop is formed). Along this vessel run delicate bundles of smooth muscle cells (Brücke) prolonged from those of the muscularis mucosa. Circularly-arranged muscle cells have also been observed by I'hanhoffer. The matrix of the villus is formed by a homogeneous reticulum, in the delicate meshes of which are placed numbers of "flattened cells of various sizes, each with an oval clear nucleus, and arranged like an endothelium" (Klein). A plexus of blood-vessels is found in this matrix; formed by an artery on one side, and a vein on the other. On the surface is a limiting basement membrane, formed by a single layer of flattened transparent endothelial plates, each with an oval nucleus (sub-epithelial endothelium of Debove and Watney). This supports the single layer of columnar epithelial cells, which covers the surface.

The epithelial cells present at the free border longitudinal

striations, which were by some believed to be due to the presence of fine pores in its substance, through which the molecular particles passed during absorption; but there is no doubt that they are formed by the longitudinal fibres of the intracellular network. The cells are connected to one another by a transparent semi-fluid cementing substance, through which, according to Watney and Klein, the minute chyle globules pass into the substance of the villus; while they subsequently find their way into the central lacteal by passing between the endothelial cells which form its wall.

Crypts of Lieberkühn.—At the base of the villi are found the openings of Lieberkühn's crypts. They are simple tubes, placed vertically in the mucous membrane, the blind extremities coming nearly into contact with the muscularis mucosæ. The epithelial lining of the crypts consists of a single layer of columnar cells, exactly similar in appearance to those on the surface of the villi, but somewhat shorter. The basement membrane here, as elsewhere, is formed of a single layer of flattened cells.

Valvula conniventes (Kerkringii).—These mucous folds, like the villi, commence to appear in the duodenum. They are formed of spiral folds of the mucous membrane, of which each passes round for about two-thirds of the circumference of the tube. They sometimes bifurcate at the ends. The two layers of each fold are tightly bound by dense submucous tissue.

These valves are useful in retarding the advance of the chyle, and at the same time afford a more extensive surface for absorption. They diminish in prominence as we pass down the intestine, and fade away about the middle of the ilium.

Glandula solitaria.—The so-called solitary glands of the small intestine are neither more nor less than lymph follicles, formed by adenoid tissue: a meshwork packed with lymphoid corpuscles, and containing a capillary plexus, while each is surrounded by a lymph-space. They cause bulging of the mucous membrane, and villi are placed on the surface of the elevation, as on other parts of the intestine.

Glandula agminata (Peyer's patches).—The groups of lymphoid follicles which form Peyer's patches are found in the lower part of the ilium, where they are placed opposite the attachment of the mesentery. They are oval in outline, with

the long axis corresponding to that of the intestine. The number usually met with is about twenty, or a little over, but in persons dying in health as many as forty-five have been found. The largest are near the ileo-coecal valve, where 200 or 300 follicles may be aggregated, forming a patch of three or four inches in length. The average is a little more than an inch. They become smaller as we trace them upwards, and in the lower part of the jejunum very small circular patches, containing three, four or five follicles, are sometimes seen. Villi are generally absent from the surface of Peyer's patches. The submucous tissue is denser here than elsewhere, and more adherent to the mucous membrane.

The structure of the individual follicles is similar to that of the solitary glands.

Peyer's patches are best developed in youth; they shrink after middle life, and disappear in old age.

The *blood-vessels* of the small intestine are extremely numerous. The arterioles which pass into the mucous membrane form capillary rich plexuses around the crypts of Lieberkühn, the meshes of which are perpendicular to the surface. An arteriole also passes into each villus, for half its length, and then breaks up into a capillary plexus (already referred to).

The *lymphatics* are very numerous, and form rich plexuses in the submucous tissue. The only notable peculiarities in their arrangement are in those of the villi, already described, and the lymph-spaces which partially or completely surround the lymphoid follicles.

Large Intestine.—The coats of the large intestine correspond to those of the small, with the addition of a few characteristics. The longitudinal fibres of the muscular coat are gathered into three bundles, which, being shorter than the gut itself, have the effect of throwing it into the form of sacculations. In the transverse septa which separate these sacculi are bundles of circular fibres, which are thin (or altogether wanting) in the intermediate part.

The submucous tissue contains as a rule more fat-cells than does that of the small intestine. The lymphoid tissue occurs as solitary follicles only, but these are much larger than in the small intestine. Meissner's plexus has larger ganglia, and smaller ganglion cells. Auerbach's plexus is also better deve-

loped, the meshwork closer, and the ganglia larger. The arrangement of blood-vessels and lymphatics is similar to that in the small intestine. The crypts of Lieberkühn are longer, more numerous, and more regularly placed, than in the upper segment of the canal.

The muscularis mucosæ consists, in most situations, of an external longitudinal and an internal circular layer. Small bundles ascend vertically from it, between the crypts of Lieberkühn.

In the rectum, the muscular fibres are no longer gathered into aggregated bundles, but the two parts of the external coat are uniformly arranged, and also very strongly developed; the circular layer being especially strong.

At the inferior extremity of the rectum the circular fibres form a special band, the *internal sphincter*, the contraction of which assists the external sphincter in maintaining the closure of the anal orifice. At the upper end of the rectum, a strong circular band "upper annulus of the rectum," *O'Beirne's sphincter*, has been described by this writer, who believed that, in the healthy condition of the bowel, this annular band prevented the descent of fecal matter into the rectum, till immediately before defæcation. Another circular band has been described at the junction of the supra- and infra-peritoneal portions of the intestine (*sphincter supérieur* of Nelaton, *sphincter tertius* of Hyrtl), to which a similar function has been ascribed.

At the extremity of the gut, the longitudinal fibres terminate partly in the pelvic fascia, while some are attached to elastic tendons, which pierce the external sphincter to end in the subcutaneous tissue around the anus (Luschka). Two flattened bundles pass, one on each side beneath the levator ani, to attach themselves to the anterior surface of the coccyx (*recto-coccygeus* of Treitz). Horner affirmed that some of the longitudinal fibres of the rectum curved round the lower border of the internal sphincter, to end in the sub-mucous tissue, but this termination has not been noticed by other anatomists.

Near the lower end of the rectum, the mucous membrane is thrown into longitudinal folds (*columnæ recti* of Morgagni), apparently by the action of the external sphincter. The remainder of the rectal mucous membrane is folded chiefly in a transverse direction. Three (sometimes four) of these folds

are more prominent than the rest, and have been specially described by Houston :—"The position of the largest and most regular valve is about three inches from the anus, opposite to the base of the bladder. The fold of next most frequent existence is placed at the upper end of the rectum. The third in order occupies a position about midway between these ; and the fourth, or that most rarely present, is attached to the side of the gut, about one inch above the anus" (Houston). These folds were believed by Houston to fulfil the mechanical use of supporting the weight of fæcal matter.

Pancreas.

In most of the broad outlines of its structure, the pancreas resembles the salivary glands, and, on this account, has been called the abdominal salivary gland (*bauchspeicheldrüse* of the German writers). The blood-vessels, lymphatics, and connective tissues are arranged in the same way. The gland is traversed from end to end by its duct (*canal of Wirsung*), which passes from the tail to the head, being somewhat nearer to the anterior surface, and receiving its tributaries in its course at right angles, like the legs of a centipede. The coats of this are similar to those of the salivary glands, and so are its lobar and intralobular branches ; the main duct and its larger branches contain in their walls some smooth muscle cells. The cells of the *lobar* ducts are shorter than those of the salivary glands, and they present very fine longitudinal striations. The lumen is comparatively larger. The *intralobular* ducts are smaller, but proportionately similar in structure. Their epithelial cells are transparent and long ; presenting the well-marked longitudinal striation of the corresponding ducts of the salivary glands. The *intermediary* ducts are minute branching tubes, the walls of which are formed by a basement membrane, lined by a single layer of flattened cells.

The alveoli, into which the intermediary tubes expand, are lined with a single layer of high columnar cells (some cylindrical, and some bluntly conical, with the truncated apex towards the lumen). The cell-substance shows two distinct zones : an outer homogeneous, which stains readily, and an inner granular, which does not stain. The nucleus is spherical, and is placed in the outer zone, at its junction with the inner.

On very accurate examination, however, the homogeneous zone is found to be made up of excessively fine longitudinal fibrils (Pflüger, Heidenhain), while the apparently granular zone is made up of a network of short thick rods (Klein).

The lining cells are connected by a thin layer of a homogeneous substance, and this substance also occupies the alveoli, "there being visible, as a rule, no lumen, or only a trace of one" (Klein). The place of the lumen is occupied by fusiform or stellate corpuscles, each with an oval nucleus—the *centro-acinar* cells of Langerhans.

When the gland is at rest in a fasting animal, its vessels are contracted, and the general color pale. When digestion commences, or when the gland is stimulated in another way, as by brushing over the duodenal orifice of the duct by a weak acid, the blood-vessels dilate so much that the arterial pulsation is transmitted to the veins, and the blood in the latter shows an almost crimson color.

The acini, after a period of rest, are found to be large in size, and the lining cells are very large; their nuclei small, crumpled, and indistinct. When secretion commences, the granular zone of the cells breaks down and is gradually cast off, forming the secretion. From his observations on the subject, Heidenhain has been led to believe that the granular material which passes away from the cells is an earlier stage of trypsin, the peptone-forming ferment of the pancreatic juice, and on this account he has given it the name of *zymogen*. During the early stage of activity, the cells stand out more prominently under the basement membrane. When the gland is exhausted and secretion ceases, the acini are found to be shrunken, the lining cells are greatly diminished in bulk, the inner granular zone having almost entirely disappeared, while the outer zone is larger than before. The nuclei are also larger and more distinct.

Liver.

The investing fibrous capsule of the liver, with its interlobular processes, was described long ago by Nathaniel Glisson, as a muscular structure, by the contraction of which the portal circulation was promoted; while, at the same time, the bile was squeezed out from the interstices of the organ as from a sponge.

Theile describes the liver-capsule as consisting of two layers: an outer, formed by white fibre-bundles, in the interstices between which elastic fibres are found, as well as branched connective-tissue corpuscles; and an inner, of more lamellar structure, the fibres of which are continuous with those of the connective-tissue of the interior of the organ.

The substance of this, the largest of the glands, is arranged in lobules of bluntly conical shape and polygonal outline (in transverse section). Each lobule is about $\frac{1}{80}$ th of an inch in diameter, and presents an axis formed by the intralobular vein, which passes from the apex to the base, where it joins the sub-lobular. The interlobular branches of the vena portæ and hepatic artery pass between the lobules and break up into lobular capillaries, which pass into the lobule and are distributed: the portal branches superficially, the hepatic, forming a thin layer inside the others, and both sets converging to join the intralobular vein. Accordingly, a transverse section of a lobule of a liver which had been injected from the three vessels (vena portæ, hepatic artery, and hepatic vein), presents three vascular zones: an external, corresponding to the portal capillaries; a median, occupied by the branches of the hepatic artery; and a central, which corresponds to the radicals of the hepatic vein. In the meshes of the capillary network are placed the hepatic cells, which are of polyhedral form, and each furnished with a clear nucleus. The diameter averages about $\frac{1}{1000}$ th of an inch.

In the interstices between the cells commence the bile-capillaries; which, according to some, have a separate wall, formed by a homogeneous membrane (Mac Gillavry, Chrzonszczewsky, Asp, Peske), while other authorities affirm that the wall is at first merely formed by the adjacent hepatic cells (Hering, Eberth, Kölliker, &c.). When traced out to the margins of the lobules, the bile vessels are found to be lined with columnar cells, resting on a delicate basement membrane, which is probably formed by a layer of endothelial cells. In the interlobular connective tissue, the larger ducts are found to be surrounded by unstriped muscle cells (Heidenhain).

The walls of the larger branches of the hepatic duct consist of a mucous membrane lined with a single layer of columnar cells, separated by loose connective tissue from a layer of unstriped muscle-cells, chiefly arranged in the form of circular bundles.



Fig. 56. Origin of bile ducts (Heidenhain).

FOOD.

The essential constituents of the human body are water, mineral substances, albuminoid matters, fats, and hydrocarbons (glycogen, sugar, &c.) ; and the aliments taken into the digestive tube must be of a nature to supply them. The aliments usually taken are formed of a mixture of several of these matters : milk contains all the essential alimentary principles ; meat contains salts, water, and albuminoids ; ordinary drinking water contains salts in solution, &c.

Simple aliments.—Besides the simple aliments essential to nutrition, some accessory ones are daily introduced into the body, such as alcohol, organic acids, alkaloids (tea, coffee, &c.), essential oils (condiments), &c. The following table gives an estimate of the quantities of the leading constituents required by an adult for 24 hours, and the proportion in which they should be mingled :—

Water .	(for 24 hours)	2,818 grammes.	(per 1000)	831
Mineral substances	"	32	"	10
Albuminoids	"	120	"	35
Fats	"	90	"	27
Hydrocarbons	"	330	"	97
Total		3,390		1,000

(1) *Water*.—Water suited for drinking should contain 20—30 per 100 of its volume of air, and this air is richer in oxygen than atmospheric air, and still more so in carbonic acid; the proportion of oxygen varies from 8—25, that of carbonic acid from 5—30; boiling expels these gases, and leaves the water of an insipid taste. The mineral substances present vary greatly in proportion; in general, water contains, per litre, 25—100 centigrammes of fixed residue, but for drinking purposes it ought not to surpass 50 centigrammes. These consist of carbonates, sulphates, alkaline chlorides, &c.

Drinking water should have an agreeable taste, and no odor. It should be clear to the naked eye, and show no inferior organisms on microscopic examination.

(2) *Mineral substances*.—The mineral substances are also indispensable in alimentation, and we have already seen the evils produced by their absence from food.

(3) *Hydrocarbons*.—These are chiefly starch and the different kinds of sugar. In this group may also be included the less important allied substances; cellulose, gums, and mucilages.

Starch.—Starch is usually met with in the vegetable kingdom, especially in the grains of the cereals and legumes. Starch grains are formed of concentric layers, alternately more or less dense, and of which the inner nucleus does not coincide with the centre of the figure. According to Nœgeli these alternate layers are formed by two distinct substances: (a) *granulose*, which is soluble in water, and gives a blue color with iodine; (b) a substance analogous to cellulose, insoluble in water, and stained red with iodine. According to Brücke, there are three different substances present: (a) *granulose*, which forms the greater part; (b) *erythrogranulose*, which stains red with iodine for which it has a great affinity; (c) *cellulose*, which is either colored yellow or not at all by iodine.

Cellulose forms the membranous cell-walls of vegetables, especially of young growths; it accordingly enters into alimentation, but its nutritive value, which has been demonstrated for herbivora by the experiments of Meissner, is more than doubtful for carnivora.

Cane-sugar.—Cane-sugar is employed in alimentation, not only in the purer form, which is extracted from the beet-root, but is also consumed daily with many vegetables: carrot, beet-root, parsnips, melon, &c.

Lactose is met with only in milk, and forms a very important article of food, especially in the infant.

Glucose (grape sugar) is present in sweet fruits: in honey, in fermented drinks (wine, beer, cider, &c). It also exists (in very small proportion) in animal food; the liver contains a little glucose formed after death at the expense of the glycogen. The muscles always contain a certain proportion of sugar (inosite).

(4) *Fats*.—The natural fats which are used as food are nearly always made up of *stearin*, *palmitin*, and *olein*; when the last predominates the fats are in the fluid state, and known as oils; in other cases they are more or less solid. The alimentary oils are usually derived from vegetable sources (olive oil, oil of almonds, &c.); butter and fats are derived from animal sources. Animal fats are sometimes isolated as butter, lard, &c., sometimes mingled with other substances, as in milk, flesh of animals, &c. They play in the nutrition of the human organism a more important part than do the vegetable oils.

(5) *Albuminoids*.—The simple aliments of this group belong, some to the vegetable kingdoms, and some to the animal. Among the former are the *gluten* which accompanies starch in the cereal grains, *legumin* (*vegetable casein*) which is met with in peas, beans, haricots, &c., and in considerable quantity. The more important animal albuminoids are the *myosin* of muscle-fibre, and the *casein* of milk.

Accessory aliments.—*Alcohol*.—This has been supposed to be a respiratory food, which, according to Liebig, was decomposed in the blood into aldehyd, acetic acid, oxalic acid, and finally carbonic acid and water. This theory was contradicted by Lallemand, Perrin, and others, who tried to prove that the greater part, if not the whole, of the alcohol absorbed, was eliminated as such by the cutaneous and pulmonary surfaces. This has, however, been disproved by more recent research, and Liebig's theory finds a large amount of support in the present day. A small proportion is found in the urine, but the pulmonary odor which is present after ingestion of alcohol does not appear to come from the alcohol itself, but from the volatile products contained in the fermented liquors. Alcohol has an indirect nutritive action, in sparing the oxidation of the azotised or non-azotised substance of the organism; in small doses it appears to diminish the excretion of nitrogen, and quantity of

urine, and retard tissue metamorphosis generally ; in large doses it has the opposite effect (E. Munk). By its oxidation it contributes to the production of heat. With regard to digestion it acts as a local stimulant to the mucous membrane of the alimentary canal. It also serves as a diffusible stimulant, which acts on the nerve centres and on the circulation.

Vegetable acids.—These acids (acetic, citric, malic, oxalic, tartaric, &c.) are met with in legumes, acid fruits, wine, acid drinks, &c). They respond to a special gustatory sensation, the need (*besoin*) of acid, which is felt from time to time, especially during thirst. They act as stimulants of the salivary secretion, and when introduced into the system are oxidised into carbonic acid.

Essential oils.—The vegetable essences (of bitter almonds, of ginger, of pepper, &c.), are much used as condiments, and seem to act in the same way as alcohol as local or general stimulants, but with special effects for each.

Generally speaking, the articles of food which are used contain many simple aliments ; some, such as milk, contain them all, and are accordingly, sufficient in themselves for the maintenance of the nutrition. But the essential constituents of food are seldom contained in the proportion required by the system ; one or other of them predominates, so that it is necessary in alimentation to mix a number of different substances. It is calculated that in 24 hours, an average adult requires 120 grammes of albuminoids, and $330 + 90 = 420$ grammes of fat and hydrocarbons.

Aliments are seldom introduced into the stomach in the state in which nature furnishes them. By the various cooking processes they are reduced to a more palatable, and, in many cases, though by no means, we regret to say, in all, they are rendered more digestible. Water, heat, and the various condiments and seasoning substances, are the agents employed in these processes. Water dissolves the soluble matters and softens the insoluble ; it is also the vehicle of most of the flavoring agents. Heat modifies the alimentary substances still more deeply, and according as the cooking is slow or rapid, as it is made by a naked fire, vapor, &c., or the action of water is added (either at the usual boiling temperature, or where it is carried beyond this by the action of fatty substances), the aliments undergo very considerable modifications.

The following table gives the proportions per 1,000 of water, albuminoids, fats, hydrocarbons, and salts, which are contained in the principal aliments :—

	Water.	Albuminoids.	Fats.	Hydrocarbons.	Salts.
Flesh (of Mammals)	730	175	40	—	11
— (of Birds)	730	200	20	—	13
— (of Fish)	740	135	45	—	15
Broth	985	—	—	—	3
Liver	720	130	35	15—20	14
Brain	770	100	100	—	11
Thymus	700	210	5	—	10
Egg	735	145	150	—	8
White of egg	845	110	10	—	6
Yolk of egg	525	170	200	—	10
Milk (Woman's)	890	40	25	44	1
— (Cow's)	855	55	45	40	5
Butter	215	15	770	—	—
Cheese	370	335	240	—	55
Wheat	130	135	20	695	20
Rye	140	105	20	615	15
Barley	145	120	25	680	25
Oats	105	90	40	735	25
Maize	120	80	50	730	12
Rice	90	50	7	845	5
Buck wheat	145	80	—	755	13
Wheaten flour	130	130	10	610	10
Wheaten bread	430	90	—	450	10
Rye bread	440	90	—	400	15
Peas	145	225	20	575	23
Kidney beans	160	225	20	540	24
Beans	130	220	15	575	25
Lentils	115	265	25	560	16
Potatoes	725	15	1	235	10
Chestnut	535	45	10	595	15
Turnip	850	15	2	135	15
Cauliflower	920	5	—	20	7
Pears	840	2	—	100	4
Apples	820	5	—	80	5
Cherries	750	7	—	100	7
Raisins	810	7	—	150	5
Wine	860-920	—	—	5	2
Beer	900	—	—	60	2

The cooking processes effect the following changes :—

The assimilable portions of the food are separated from the non-assimilable (elastic tissue, cellulose, &c.) ;

The aliments are rendered more accessible to the digestive juices (by division, penetration of the water, &c.) ;

The soluble parts are dissolved, and are then, of course, absorbed more rapidly ;

The essential aliments present in the articles of food are concentrated and condensed (as in extract of meat, &c.) ;

The digestive secretions are stimulated (by acids, alkalies, alcohol, &c.) ;

The aliments are rendered more agreeable to taste and smell ;

The various alimentary substances are mingled together in such a manner as to develop their digestibility, and their gustative properties ;

The succession of the aliments in a meal is so arranged that they mutually aid the digestion of one another ;

In a general way, the digestive capacity is increased in a double fashion ; there is increased digestibility of the food, and on the other hand, there is an increase of the digestive secretions.

THE DIGESTIVE JUICES.

These fluids are secreted by the glands, of which the microscopic anatomy has been already described. They are five in number : saliva, gastric juice, bile, pancreatic juice, and intestinal juice.

Saliva.

The mixed human saliva is a fluid slightly opaline, inodorous, frothy and more or less viscid. Its reaction is alkaline ; the alkalinity being due to the presence of the bicarbonates and the earthy phosphates. Its specific gravity is 1.004—1.009.

The saliva first secreted after a long fast is acid, but this acidity is due to decomposition, although some believe that a really acid secretion is poured out by the glands at first. The microscope shows epithelial cells, salivary corpuscles, and sometimes inferior organisms (*leptothrix buccalis*).

The daily quantity of this secretion in man is difficult to calculate with any degree of accuracy, but is said to vary from 300 to 1,500 grammes. There is but a small quantity formed during the intervals between meals, but during mastication the secretion is very active, varying, however, with the nature of the food. The submaxillary and sublingual secretions are continuously formed in moderate quantity, the secretion being

unconsciously swallowed; the great increase while eating is chiefly of the parotid saliva.

The secretion is excited by gustatory stimuli (acids, bitters, &c.); by mental emotions (sight of food, odors); by nerve stimulation; by the presence of food in the stomach; by the movements of mastication, &c. It has been observed that chewing movements of one side markedly increase the secretion on that side; this is easily observed in such animals as the horse. Different stimuli seem to influence the secretion of the different kinds of saliva. Visual impressions and the movements of mastication do not seem to act on the submaxillary secretion; which is, however, very sensible to gustatory impressions (Schiff). Some substances, especially atropin, arrest the secretion.

When a quantity of saliva is placed in a vessel at rest, it divides into three parts: a superior layer, viscid and frothy; a middle, limpid and slightly viscid; and an inferior layer formed by a greyish-white deposit (epithelial cells and salivary corpuscles).

Saliva is made turbid by heat, showing the presence of albumen; alcohol, tannin, corrosive sublimate, &c., cause the appearance of a flocculent precipitate. It is tinged red by the perchloride of iron (sulphocyanide of potassium). Saliva decolorises the iodide of starch.

Chemical composition.—Mixed human saliva contains:

- (1) Albuminous substances; traces of albumin, and of mucin;
- (2) A peculiar ferment (*ptyalin, salivary diastase*); traces of pepsin;
- (3) Fats;
- (4) Traces of urea; sometimes leucin;
- (5) Sulphocyanide of potassium or of sodium;
- (6) Salts; especially chlorides of sodium and of potassium; alkaline and earthy phosphates; carbonate of lime; phosphate of iron; nitrate of ammonium (Schönbein);
- (7) Gases; especially carbonic acid, with a little oxygen and azote.

The *ferment* of saliva (*ptyalin*) is best prepared by Cohnheim's method. In this proceeding a quantity of saliva is first collected by exciting the buccal mucous membrane by inhaling the vapor of æther; it is then strongly acidified by phosphoric

acid ; lime water is added till the solution becomes alkaline ; a precipitate of basic phosphate of lime falls down, which carries down with it the albuminoids and ptyalin. This is removed by filtration, and the residue is washed with water, which removes the ptyalin, and leaves the albuminoid substances on the filter. The washings are treated with alcohol, and a white flocculent precipitate is obtained, which is dried in a vacuum with sulphuric acid. A greyish-white powder is obtained, which is formed by the ptyalin, mixed with phosphates. It is separated from the latter by dissolving in water, precipitating by absolute alcohol, washing with dilute alcohol, then with a little water, and finally drying at a low temperature.

The ptyalin so obtained is a nitrogenous substance, but not albuminous ; it is easily soluble in water and in glycerine. It transforms starch and glycogen into glucose. It acts best in a weakly acid medium, but the action remains when the solution is made neutral or even feebly acid ; an excess of alkali or acid destroys it. Its action is retarded by the product of its own activity (glucose) ; when it collects in considerable quantity, the solution must be diluted before any further transformation takes place. By adopting this plan, an indefinitely large quantity of starch may be converted into glucose. The evidence of later researches goes to prove that the action of ptyalin is not affected by the presence of any of the other digestive juices.

According to Cl. Bernard, and some other observers, ptyalin does not pre-exist in human saliva, but is the product of an alteration which takes place in the buccal cavity.

The presence of sulphocyanide is not constant, but the conditions of its presence have never been ascertained. Some have supposed it to be due to the presence of nicotin, and, accordingly, only found in the saliva of tobacco-smokers ; by others it has been supposed to be due to dental caries ; it is, however, independent of both conditions.

The following are a series of analyses of mixed human saliva :

		Simon.	Berzelius.	Neriches.	Jacobowitsch.
Water	(per 1,000)	991.22	992.9	994.10	995.16
Solids	„ ..	8.78	7.1	5.90	4.84
Ptyalin	„ ..	4.37	2.9	1.42	1.34
Mucin	„ ..	1.40	1.4	2.13	1.62
Sulphocyanide	of				
potassium	„ ..	—	—	.10	.06
Salts	„ ..	—	1.9	2.19	1.82

The proportion of chlorides is .71 and that of phosphates .86 per 1,000. The proportion of ptyalin of the above analyses is somewhat large ; it seldom passes 1.12 per 1,000.

Submaxillary saliva.—This fluid is more viscid than the parotidean ; it contains mucus, and gelatinous corpuscles. Its specific gravity (1.002—1.003) is less than that of the parotid saliva (Eckhard) ; the contrary is the opinion of Oehl, who makes it to be 1.010—1.016 before a meal, and increasing soon after to 1.020—1.025. According to the same author, its quantity would be greater than that of the parotid saliva in the proportion of 3 : 1. On exposure to the air it becomes more viscid, and forms a flocculent precipitate, which does not appear in air deprived of carbonic acid (Eckhard). The addition of corrosive sublimate makes it gelatinous, without causing turbidity. It contains ptyalin, and according to some (Oehl and Sertoli) sulphocyanide of potassium, but in smaller quantity than does the parotid secretion. Many chemists, however, deny its presence.

Chorda saliva.—The chorda saliva (*trigeminal saliva*) obtained by stimulation of the chorda tympani nerve, is a clear, limpid fluid (excepting the first few drops), and has a very decided alkaline reaction. Sp. gr. = 1.0039—1.0056. It contains no morphological elements. The presence of ptyalin is very doubtful ; it exists only in very small quantity, if at all. It is secreted in very large quantity.

Sympathetic saliva.—The submaxillary saliva obtained by stimulation of the sympathetic is viscid, very opaque, and flows in long strings from the duct. Sp. gr. = 1.0075—1.0181. It contains a great proportion of morphological elements, especially gelatinous masses, which seem to be broken-up gland cells. It contains salivary corpuscles analogous to leucocytes, and granular corpuscles of undetermined nature. It contains albumin, and a large proportion of mucin, and is of alkaline reaction. The inorganic elements are the same in both these kinds of saliva. These are alkaline chlorides, phosphates and carbonates of lime and magnesia. Some free carbonic acid is also present.

The quantity of the sympathetic secretion is always small and soon stops altogether ; if the secretion be continued, the gland undergoes a true fatty degeneration.

Parotid Saliva—The parotid saliva of man is a thin, colorless, limpid fluid, of alkaline reaction. Its specific gravity

varies from 1.0061 to 1.0088 (Hoppe-Seyler); or, according to Beaunis, 1.031 to 1.043. The first drops are usually turbid, and the reaction feebly acid, but after a short time the secretion becomes as clear as water, and the reaction faintly alkaline. According to Astaschewsky, the acidity reappears, and is at a maximum, about two hours after eating. The daily quantity has been calculated at 80—100 grammes (Oehl). It is increased by the movements of mastication, also by the introduction of acids into the mouth; sweet substances do not appear to have any such influence.

Parotid saliva does not contain morphological elements. When exposed to the air it becomes turbid from the precipitate of carbonate of lime, which falls down when the carbonic acid is given off. Heat causes more marked turbidity (albumin and carbonate of lime); mineral acids cause effervescence; it gives the reaction of sulphocyanide of potassium, but this reaction is sometimes masked by other substances (Dalton, Sertoli). It contains neither ptyalin nor mucin. Other albuminous substances are present, also traces of urea and inorganic salts, especially alkaline chlorides, and bicarbonate of calcium, with traces of phosphates and alkaline sulphates. Some assert that a volatile fatty acid is present.

Heidenhain has described (in his researches on the dog and rabbit) two kinds of parotid saliva, a cerebral (produced by stimulation of the glosso-pharyngeal), and a sympathetic. Both are clear, transparent, and never ropy during secretion; the cerebral secretion is much more copious, and contains a smaller proportion of solids. Heat makes the sympathetic secretion gelatinous, while it makes the cerebral merely turbid.

Sublingual Saliva.—This secretion has been obtained in man by Oehl, by introduction of a canula. It forms a clear, viscid, and very alkaline fluid. The quantity was, however, too small to admit of full examination of its qualities.

Salivary Secretion.—Submaxillary.—This is, of all the secretions, the one whose mechanism has been most completely studied, especially in the dog. The two kinds of cells lining the acini in this animal have been already described. The mucous cells furnish the mucin, and are believed by Heidenhain to be completely destroyed by the secreting process, while Ranvier and Renaut believe that they merely empty their contents into the lumen of the acinus, to be carried off as the secretion.

The part taken in the secretion by the protoplasm cells of the crescent of Gianuzzi remains still unsettled. According to Heidenhain and Lavdowsky, they multiply during the secretion so as to take the place of the mucous cells; but Ranvier and some other authorities regard them as completely distinct varieties. The protoplasmic cells are believed by Bufalini to be concerned in the production of the salivary secretion, properly so called, and probably in the formation of the salivary ferment.

The secretion of the submaxillary gland is influenced by two chief factors: the *circulation*, and the *nervous system*.

The *circulation* has been studied with great care by Cl. Bernard. The quantity of blood which flows through the gland is much increased during the time of activity; when at rest, the venous blood returning from the gland is seen to be dark in color, and scanty in proportion, but during activity scarlet blood passes in large quantity into the veins, and even receives a pulsation transmitted from the arteries.

Two varieties of nerves influence the secretion: the *vascular* and the *glandular*, and of the former kind there are two varieties, the *vaso-constrictor* and *vaso-dilator*. The vaso-dilator nerves come from the chorda tympani, stimulation of the peripheral end of which causes dilation of the vessels, with great increase of the blood-pressure; the blood flowing through the vessels with increased velocity as well as augmented quantity. The venous pressure increases from 10 to 15 mm. of mercury at the time of stimulation. Section of the nerve produces the opposite effect, the venous blood remains dark, even when vinegar is applied to the tongue. Bidder attributes the redness of the venous blood during glandular activity, to loss of water in passing through the gland, and the consequent proportional increase of solid matters. The vaso-constrictor nerves come from the sympathetic, and stimulation of the sympathetic filaments has an effect on the circulation exactly opposite to that produced by stimulation of the chorda tympani.

The *glandular* nerves act more directly on the epithelial cells themselves. They are contained in the same sheaths as the vaso-motor nerves, and are believed by Heidenhain to consist of two sets: *trophic* or *muciparous*, and *secretory*. Their influence may be separated by physiological experiment. Injection into Wharton's duct of a weak solution of car-

bonate of soda, hydrochloric acid, or sulphate of quinine, renders all secretion impossible, although stimulation of the chorda tympani causes the same increase of vascularity as before. The increased exudation of blood-plasma, under the increased vascular pressure, causes œdema of the gland from accumulation in the circum-acinar lymph-spaces. Certain poisons, such as atropin, have a similar effect of paralysing the glandular nerves without affecting the vaso-motor. The peculiar influence of these nerves explains the apparently paradoxical conditions observed by Ludwig, who found the pressure of the saliva in Wharton's duct greater than that of the blood in the carotid artery, and the temperature of the former fluid 1°.5 higher than that of the latter.

The peculiarities of the two kinds of saliva produced by nerve stimulation have been already mentioned. According to Heidenhain, the character of the so-called sympathetic saliva holds good only for the first portions secreted, and after some time it becomes fluid, like that of the chorda tympani. He also completely denies the occurrence of the colloid degeneration of the gland observed by Kühne after prolonged stimulation of the sympathetic. According to Langley, the sympathetic saliva of the cat is even more fluid than the chorda. The nature of the influence of the sympathetic on the secretion is not quite understood. Czermak and Petrowsky look upon it as an inhibitory action. This view has been controverted by most authorities, especially by Bidder, who makes its influence to consist in vascular constriction, and a modification of the adhesion between the walls of the vessels and the contained blood. Kühne believes the two nerves in this case to exercise a mutual inhibitory influence. Heidenhain, on the other hand, considers that their action is entirely similar, differing in degree, but not in kind; each enclosing both varieties of glandular fibres, but in unequal proportions.

In the physiological state, salivation is always the result of reflex action. The stimulus is conveyed from the periphery to a salivary nerve-centre, from which it is reflected along the secretory nerve-fibres to the gland. The initial stimulus may be conveyed by different sets of nerves: (1) *gustatory*, as in ordinary sensations of taste, especially acids; (2) *olfactory* (certain odors); (3) *nerves of tactile sensibility* (mechanical irritation, friction, movements of mastication, talking, nausea, &c.); (4) *gastric nerves* (arrival of food in the stomach, or mechanical irritation of the gastric mucous membrane). The initial stimulus may proceed from the nerve centres, as in case of the salivation produced by the sight or thought of food.

Submaxillary salivation is produced experimentally by stimu-

lation of the nerve-trunks already mentioned : gustatory, glosso-pharyngeal, &c. Stimulation of the vagus trunk has a similar effect (Oehl, Cl. Bernard), but this has been attributed to the action of its sympathetic fibres. It has been observed to follow stimulation of the central end of the divided sciatic nerve (Owsjannikow, Tschiriew), a result of which the cause is very obscure ; it was believed by these observers to be due to vasodilator reflex, exercised through the chorda tympani, but this is disproved by the fact that the influence of atropin stops the secretion, while the vascular dilation persists (Grutzner, Chtapowski).

Inhibition of the reflex salivary secretion is sometimes seen, as in the well-known phenomenon of drying of the mouth produced by intense fear. The salivary secretion is also arrested by opening the abdomen of an animal, and drawing a loop of intestine through the wound ; this influence is probably due to irritation of the sensory nerves of the viscera.

The position of the salivary centre for the submaxillary gland has not been definitely settled. Stimulation of the floor of the fourth ventricle, at a point just in front of the point of diabetic puncture, has been found to produce salivation (Cl. Bernard) ; also stimulation of the neighborhood of origin of the facial nerve (Eckhard). But the centres would seem to be placed higher up ; stimulation of the base of the brain in the floor of the third ventricle produces an abundant flow of saliva (Beaunis), also stimulation of the cortex cerebri in the neighborhood of Hitzig's facial centre (Lepine, Eulenburg, Landois), but the latter result has been contradicted by Kulz and Eckhard.

Whether the submaxillary ganglion forms a local reflex centre for the submaxillary secretion is a question which has elicited much discussion. Bernard has answered in the affirmative : he divided the gustatory nerve, both above and below the ganglion, taking care to preserve the branches which go to the latter from the gustatory and chorda tympani nerves, and then divided the sympathetic, and having in this way separated the ganglion from the nerve-centres, he still found that stimulation of the peripheral end of the divided gustatory produced salivation. The same effect is produced, although not so easily, when the lingual mucous membrane is excited (by æther, electricity, &c.). This salivation ceases immediately on division of the gustatory nerve, between the ganglion and the tongue. Schiff has controverted these results, and attributes the salivation so produced to errors of observation (using too strong currents, which escaped upon the nerves &c.). They have also been denied by Eckhard. Bidder admits the result,

obtained by Cl. Bernard, but explains by the anatomical arrangement of the nerve-fibres. He has traced fibres in the gustatory trunk, which pass from the mucous membrane to the ganglion, and do not degenerate after section of the lingual trunk. He differs, however, from Bernard, in not regarding them as directly excitable.

Certain substances excite the salivary secretion; especially pilocarpin (jaborandi), eserine (calabar bean), muscarin, nicotin, curara, &c. Other substances arrest it, such as the narcotics (especially atropin, daturin, cicutin, &c.; also nicotin, when given in large doses. According to Luchsinger and Jänicke, the carbonic acids of the blood acts as a stimulant to this as well as other secretions. The secretion is arrested in dyspnoea, and this result has been attributed by Sokolowin to deficiency of oxygen.

Parotid secretion.—The parotid gland presents acini lined throughout with granular protoplasmic cells; no mucous cells are present.

The influence of the circulation and of the nervous system on the parotid secretion is similar to what we have described in case of the submaxillary. The *vaso-dilator* nerves come from the glosso-pharyngeal (Jacobson); stimulation of the nerve of Jacobson causes a copious flow of venous blood, the color of which approaches the arterial hue. The amount of independence of the circulation is, however, markedly shown by the fact that, after decapitation, the parotid of the sheep may continue to secrete for a quarter of an hour (Brettel). The glandular nerves are from two sources: *cerebral* (through facial and, perhaps, glosso-pharyngeal) and *sympathetic*. The parotid-fibres of the facial nerve pass from the geniculate ganglion through the lesser superficial petrosal, to the otic ganglion, from which they proceed with the auriculo-temporal nerve to the gland. This course has been demonstrated by an elaborate series of experiments: section of the facial trunk below the stylo-mastoid foramen does not stop the salivary secretion, nor does extirpation of Meckel's ganglion, or section of the chorda tympani. But section of the lesser superficial petrosal, or ablation of the otic ganglion, has the effect of arresting the secretion at once.

The glosso-pharyngeal nerve also supplies filaments to the parotid gland (Loeb, Heidenhain). Loeb found that, after intracranial section of this nerve, stimulation of the buccal mucous membrane was followed by no increase of the parotid secretion. Heidenhain found in the dog that stimulation of the nerve of Jacobson caused the pressure in Steno's duct to rise from 70 or 80 mm. of mercury to 106 or even to 118 mm.

Some authors (Grünhagen, &c.) deny that the sympathetic has any influence on the parotid secretion. Most, however, admit with Claude Bernard and Heidenhain that it has; that stimulation produces a limited flow of parotid saliva. According to the latter, the sympathetic filaments, to which this effect is due, are neither glandular fibres, properly so-called, nor vaso-motor fibres, but *trophic* fibres, under the influence of which the organic substance forms in the glandular cells.

Sublingual secretion.—The activity of this gland appears to be under the same influences as the submaxillary and parotid. Like the submaxillary it is a muco-salivary gland.

Theories of the salivary secretion.—Numerous theories have been offered in explanation of the nature and mechanism of this secretion. The phenomenon of secretion has been referred to molecular attraction (Hering), to solution of the organic substances contained in the cells (Ewald), to electrolytic decomposition (Ranke), to simple glandular diffusion (Ludwig), &c.; but all these theories are imperfect, and any one, even if true, could only apply to one of the conditions of secretion. Heidenhain's hypothesis, which separates the glandular nerves into secretory and trophic, seems to embrace a large proportion of the facts; but even this can only be accepted provisionally. The influence of the trophic fibres would account for the accumulation of material in the glandular cells during rest, which is discharged into the lumen of the acinus during the activity of the secretory fibres.

Physiological Uses of Saliva.

During the intervals of digestion the great use of the saliva is simply to moisten the buccal mucous membrane. It has been suggested that the presence of the sulphocyanide of potassium may prevent decomposition of the particles of food which remain between the teeth, &c. As the secretion is continuous (although not in large quantity), it is constantly exciting acts of deglutition, by which the Eustachian tube is laid open, and allows the cavity of the tympanum to communicate with the external air. In this way salivation indirectly aids in regulating the organ of hearing, by maintaining the normal pressure of the air within the tympanic cavity.

During the process of digestion the saliva has three chief

uses : (1) it dissolves soluble matters, and may, by its alkalinity, dissolve a small proportion of the albuminoids ; (2) it mixes with the food and facilitates mastication, and more especially deglutition, while it renders it more easily permeated by the other digestive juices ; (3) it changes starch and glycogen into glucose. The drier the food, the greater the quantity of saliva secreted ; while ligature of the salivary ducts of an animal renders mastication slow, and deglutition almost impossible (when the food is dry).

The amylolytic action of saliva has been generally explained by saying that the starch is first converted, either partially or wholly, into dextrin, after which the latter is further changed into grape-sugar by the addition of water (hydrolytic action). Recent researches have, however, shown that the phenomenon is much more complex. Starch, under the influence of the salivary ferment (*ptyalin*), forms several substances : (1) soluble starch (*amidulin* of Nasse, *amyloextrin* of Naegeli), which is stained of a vinous red by iodine ; (2) *erythroextrin* of Brücke, which is colored red by iodine ; (3) *achrooextrin*, which is not stained at all by iodine ; (4) *maltose* ; (5) *glucose*. The ultimate products should be (3), (4), and (5) (Musculus, Gruber, V. Mering). Of achrooextrin, three varieties exist, α , β , γ , which differ in their rotatory and reducing power ; the third has been described by Seegen, under the name of *dystropoextrin*. Nasse asserts that the sugar formed has less reducing power than glucose and proposes to name it *ptyalose* ; but, according to Musculus, this ptyalose is but a mixture of dextrin and maltose, with some traces of glucose.

The peculiar action of saliva on starch is due to the ptyalin, which acts the part of a ferment. But its action is limited ; it ceases after some time, and a definite quantity of saliva can alter but a certain proportion of starch. The whole of the altered starch does not form sugar ; about 25—30 per cent. is changed into dextrins.

Its activity is greatest at a temperature of 38°—41°C. (100°.4—105°.8 F.). The action is slowed by lowering or raising the temperature ; at the freezing point it ceases entirely, and at 70°C. (158° F.) the ptyalin is completely destroyed. Its activity is greatest in a feebly alkaline medium, but it continues when the fluid is neutral, or even slightly acid ; increase of the alkali, or acid, slows and then stops it ; while concentrated solutions

instantly destroy it. When the proportion of glucose formed reached 1.5—2.5 per 100, the action of ptyalin ceases, but commences again when the fluid is diluted.

Saliva does not change cane-sugar into glucose, and, indeed, its action on starch is much less than it was formerly believed to be. Claude Bernard even went so far as to deny the sugar-making action of saliva, and looked upon its functions as purely accessory in their nature to mastication (parotid saliva), gustation (submaxillary), and deglutition (sublingual).

Gastric Juice.

The gastric juice is a colorless, limpid fluid, of an odor entirely *sui generis*. The reaction is strongly acid, when pure ; but this acidity is diminished by the admixture of mucus or saliva, often so much that the fluid found in the stomach is decidedly alkaline. The pure juice is very fluid, and its specific gravity is but a little more than that of water (1.001—1.003). The quantity of gastric juice secreted daily is difficult to calculate ; but it has been estimated at six kilogrammes (13 or 14 litres, Foster).

When filtered, so as to remove the epithelial debris, the gastric juice keeps for a long time without decomposing. When concentrated, it acts upon marble with disengagement of small bullæ of carbonic acid. When heated, its activity is destroyed, but there is no precipitate formed. It yields a small precipitate to alcohol ; also to bichloride of mercury or acetate of lead.

Chemical composition.—Gastric juice contains ten parts per 1000 of solids, of which one-third is made up of organic substances. The following constituents are present, besides water :—

- (1) A soluble ferment, *pepsin* (3 per 1000) ;
- (2) A free acid, very probably *hydrochloric* (1—2 per 1000) ;
- (3) *Mineral salts* (2 per 1000), consisting chiefly of the chlorides of potassium and sodium, a small quantity of chloride of calcium, and of the phosphates of magnesium and of iron.

Pepsin has not been obtained in a state of absolute purity. The best method is that of Brücke. He digests the gastric mucous membrane at 40° C. (104° F.) with dilute phosphoric acid ; the fluid is neutralized by the addition of lime ; this causes the precipitation of neutral phosphate of calcium, which carries down the pepsin with it. The precipitate is then

washed and dissolved in dilute hydrochloric acid; a solution of cholesterin in four parts of alcohol and one part of æther, is added; the cholesterin is then precipitated with the pepsin. The precipitate is washed with water, and dissolved in æther. The supernatant æther is then decanted, and the remaining aqueous solution contains the pepsin, which is obtained by evaporation. Separated in this way, it is found to be a yellowish powder, soluble in water and in glycerine, insoluble in alcohol. It is not diffusible even when there is an acid or fibrin in the external liquid (Hammarsten). The dried powder may be heated to 110° C. (230° F.) without losing its properties, but in solution it has less resisting power. At 40° C. (104° F.) it is changed into a less active substance, *isopepsin* (Finkler), and at 80° C. (176° F.) it loses all its power. It is precipitated from solution by the neutral and basic acetates of lead, but is not thrown down by nitrate of silver, tannin, acetic acid, or ferrocyanide of potassium.

The chemical composition of pepsin is still unknown. It is generally admitted to be a nitrogenous substance, but some authorities, and especially Schiff, look upon it as a ternary compound.

The acid of the gastric juice has been a source of much discussion; the nature of the acid itself has been disputed as well as its conditions—free or combined.

A. *The gastric acid is a free acid.* (a) *Hydrochloric.*—That the acidity of the gastric juice is due to free hydrochloric acid, has been admitted by Braconnot, Prout, C. Schmidt, Rabuteau, &c., and the presence of the acid has been demonstrated by elaborate experiments. Prout obtained hydrochloric acid by distillation of the gastric juice; but this apparently conclusive proof of its existence was invalidated by Lehmann, who showed that distillation of the metallic chlorides with lactic acid produced hydrochloric acid. Schmidt has shown that the quantity of chlorine present is always more than enough to saturate the bases, but the objection has been made that, in his method, calcination of the chloride causes a certain proportion to be lost by volatilization, and so diminishes the quantity of the base. Rabuteau saturates the gastric juice with recently prepared quinine; the undissolved quinine is then separated by filtration, the fluid is evaporated, and the residue is treated with amylic alcohol, which dissolves the hydrochlorate of quinine, but not the chloride of sodium. He has found the salt in the residue, and the proportion of chlorine corresponds to 2.5 per 1000 of the gastric juice. Several other modes of examination of still more complex nature have been devised.

(b) *Lactic.*—According to some eminent authorities (Lehmann, Claude Bernard, Smith, Laborde, &c.), the acidity is due to the presence of free lactic acid. Some of these observers endeavored to demonstrate the presence of lactic acid, while others merely denied the existence of hydrochloric, and supposed the presence of lactic.

Lehmann obtained lactate of magnesia, by the addition of magnesia to the gastric juice of the dog. Laborde affirms the existence of lactic acid on the following grounds: (1) If starch be treated with dilute hydrochloric acid at a temperature of 150°—155° C. and a pressure of five atmospheres, it is changed into glucose; transformation does not occur under the influence of gastric juice or of lactic acid. (2) Hydrochloric acid has the effect of changing cane-sugar into glucose, with double the rapidity exercised by lactic acid, or by gastric juice. (3) If the three fluids—hydrochloric acid

(1—1000), lactic acid (1—1000), and gastric juice,—be taken and treated with sulphate of aniline, there is no change of color. If a mixture of bin-oxide of lead and water be added to each, the second and third are found to give the same wine-red color, while the first yields a mahogany color.

B. *The acid of the gastric juice is in a state of combination.* The following are the chief arguments in favor of this view : (1) If gastric juice and a solution containing the same proportion of hydrochloric acid be submitted to dialysis, it is found that the former dialyses much less easily than the latter (Ch. Richet). (2) Berthelot has shown that, if an alkaline acetate be placed in presence of hydrochloric acid, the chlorine combines with the metal and acetic acid is set free ; gastric juice, on the other hand, displaces but half (Ch. Richet). The action of gastric juice on starch and on cane-sugar, as mentioned above, may also be used as arguments in favor of this theory. With regard to the nature of the combination the following views have been advanced :—

(a) *The acid is found in the state of phosphate of lime.* This view was advocated by Blondlot, but has ceased to exist. The acid phosphate of lime came from digestion of bone.

(b) *The acid is combined with pepsin, as a pepto-hydrochloric acid* (Schiff, Ch. Schmidt, V. Wittich). This opinion is based chiefly on the fact that pepsin does not act on albuminoids, except when acidulated. There are some other minor arguments that have been advanced in favor of this hypothesis, but they are of very doubtful value. We must also remember that this acid has never been isolated.

(c) *The hydrochloric acid is combined with leucin* (Ch. Richet). Richet, believing that he had demonstrated that this acid existed in a state of combination, was led to seek for the presence of a weak base, and found that he could extract leucin (and tyrosin), not from the gastric juice, but from the gastric mucus. But it is now known that leucin and tyrosin are formed during the peptic digestion of albuminoids, and that they are yielded by all animal tissues.

From the evidence collected on the subject, we can only conclude that the balance is in favor of the idea, that the acid of the gastric juice is hydrochloric ; and that it exists in a free state, as there is no real proof of its combination.

Schiff admits the existence of two varieties of gastric juice : the *peptic* and the *acid* ; the first is formed during digestion, and the second afterwards, when the store of pepsin is exhausted. The latter, then, cannot reappear till the peptogenous substances have again charged the stomach with pepsin. Recent researches have demonstrated the existence of three varieties of gastric secretion :—

(1) *Pyloric juice.*—This is a perfectly clear, transparent fluid, of alkaline reaction, and somewhat ropy consistence. At the temperature of the body it coagulates fresh milk (in 15—60

minutes), without the production of acidity. According to Hammersten, this action (coagulation of the casein) is due to the presence of a special ferment, to which he has given the name of *lab*. There is no amylolytic ferment present. The percentage of solids is 1.065—2.05.

(2) *Gastric juice*, properly so-called.—This comes chiefly from the cardiac end, and great curvature of the stomach, and nearly corresponds to the description already given of the ordinary mixed secretion. It is usually quite clear (sometimes a little opalescent), very strongly acid, and containing about .45 per cent. of solid matters (.20—.85). The proportion of acid averages .520 per cent. (.463—.580). It is made very slightly turbid by heat, and on addition of alcohol throws down a small flocculent deposit. It is not affected by strong nitric acid; is made slightly turbid by bichloride of platinum, more so by acetate of lead, and still more by tannin. It contains pepsin, and traces of organic substances.

(3) The *gastric mucus*, such as is found on the surface of the stomach during fasting, is an alkaline, ropy fluid, almost quite clear, but showing a slight greyish-white tinge, when mixed with epithelial debris. It is rich in mucin.

The secretion of the gastric juice is intermittent, except in those animals, such as the rabbit, in which the stomach always contains food. In the carnivora, the acidity is greater than in herbivora or in man. The same is true of the pepsin. The secretion is excited, either by direct irritation of the mucous membrane, or by stimulation reflected from a distance. Any mechanical irritation causes secretion of gastric juice, not only at the point touched, but over the whole surface. Swallowing of æther, or of cold water, also produces the same result. Alkaline fluids are the most powerful stimulants, and especially saliva, the swallowing of which with the food acts as a physiological stimulant, during the time of gastric digestion. Gustatory impressions also act as stimuli to the secretion of the gastric juice. All these causes act more rapidly and effectually after the stomach has been emptied for some time. At the end of the act of digestion, when the glands are exhausted, stimulation of any kind causes only an increase of gastric mucus, or the secretion of an acid fluid containing no pepsin.

The following table gives four analyses of gastric juice, after Schmidt :—

Per 1000 parts.	Man. Mixed with saliva.	Dog. Without saliva.	Dog. with saliva.	Sheep.
Water	994.4	973.0	971.2	986.15
Solids	5.6	27.0	28.8	13.85
Organic matters ...	3.19	17.1	17.3	4.05
Chloride of sodium ...	1.46	2.5	3.1	4.36
Chloride of potassium	.55	1.1	1.1	1.52
Chloride of ammonium	—	.5	.5	.47
Chloride of calcium...	.06	.6	1.7	.11
Free acid	.20	3.1	2.3	1.23
Phosphate of lime ...	.12	1.7	2.3	1.18
Phosphate of magnesia		.2	.3	.57
Phosphate of iron ...		.1	.1	.33

Secretion of gastric juice.

As already observed, the gastric secretion contains three distinct kinds of fluid: peptic, pyloric, and mucus. The peptic (cardiac) glands secrete the first-named constituent; the second is the product of the pyloric glands, while the third is furnished by the epithelium of the mucous membrane.

(1) *Secretion of the gastric (peptic) juice.*—The two varieties of cells which line the so-called peptic (cardiac) glands have been already described. The part taken by each in the secretion has been a good deal discussed of recent years. The external cells, *principal* cells (*Hauptsellen*) of Heidenhain, *adclomorphous* (indistinct) cells of Rollett, contain mucus and do not stain with carmin. They are clear, transparent, nucleated cells, and form a complete lining for the tube in which they are placed. The outer cells, *parietal* cells (*Belegzellen*) of Heidenhain, *delomorphous* cells of Rollett, contain no mucin, while they stain with carmin. They are large, granular, nucleated cells; oval in outline, with the long axis parallel to that of the tube, and forming an incomplete layer in contact with the basement membrane, beneath which they bulge out prominently during digestion, so as to give it a nodular appearance. These cells were formerly believed to have the special function of forming the pepsin, on which account they were called peptic cells. The contrary opinion has been recently advanced

by Heidenhain, who has found the principal cells disappear by auto-digestion when placed in contact with dilute hydrochloric acid, while the parietal cells merely become distended. The inner cells also swell up at the commencement of secretion, and diminish at the end of the process; and, according to Heidenhain, there is a direct proportion between their volume and the quantity of pepsin formed. In the frog, the pepsin is formed by the œsophageal glands, which are lined only by cells analogous to the principal cells; while the parietal cells are found in the glands of the stomach, which only yield an acid fluid containing no pepsin (Swiescicki, Partsch). In the dormouse, the principal cells disappear almost completely during hibernation, when the activity of the stomach is suspended. Basing his opinion on these facts, Heidenhain believes that the principal cells form the pepsin, while the secretion of the hydrochloric acid is the special function of the parietal cells. Some authors, however (and especially V. Wittich), vigorously oppose the views of Heidenhain; and, according to Gottfried Herrendörfer, the principal cells are derived from the others by metamorphosis.

It is probable that the pepsin is united to the albuminates of the gland-cells, and removed by the acid; for, if all the pepsin of a portion of the gastric mucous membrane be removed by water or glycerine, treatment by addition of dilute hydrochloric acid is followed by the formation of a fresh quantity. It is generally supposed that its formation is preceded by that of a *pepsinogenic substance* (*propepsin* of Schiff). This substance is, in its turn, formed from *peptogenic substances*, which are taken into the blood by absorption. The chief of these substances are dextrin, bone, gelatin, and peptones. If the peptogenic substances are not furnished with the food, pepsin will not be formed. According to Bacelli, it is the spleen which furnishes the pepsin to the stomach; he has found in this organ a substance rich in pepsin, which digests albumin. His results, however, been denied by Mosler.

The *seat* and *mechanism* of the formation of the acid are equally obscure. It was observed by Brücke that the surface of the mucous membrane was the only portion which gave an acid reaction during the secretion of gastric juice, and this observation was confirmed by the ingenious experiment of Bernard, who found that on injecting ferrocyanide of potassium into one vein, and lactate of iron into another, the coloration of Prussian blue, which

forms but in an acid medium, is seen only on the surface. Brücke refers the formation of the acid to nervous influence, which decomposes the chlorides, and directs the acids towards the free surface, while the bases are kept in the deep parts. Ralfe has suggested that it is due to electricity: on separating, by a porous diaphragm in a U-tube, a solution of bicarbonate of soda and of neutral phosphate of soda, and passing a weak electric current through, he has found the liquid assume an acid reaction at the positive pole (acid phosphate being formed), while the alkalinity increased at the negative pole. If the chloride be substituted for the neutral phosphate in this reaction we should have the following:



These ideas are, of course, purely hypothetical.

The seat of the formation of the acid is still doubtful, but the idea of Heidenhain, that it is formed by the parietal cells, appears to have a great many things in its favor. The pyloric glands, in which these cells are absent, secrete an alkaline liquid, and such cells are found everywhere that an acid secretion is formed.

Pyloric secretion.—The secretion of the pyloric glands is continuous, contrary to what holds good of the cardiac tubes. The existence of pepsin has been greatly disputed, but its presence is now generally acknowledged. According to V. Wittich, the pepsin comes from the *cul-de-sac*, and passes into the pyloric glands by imbibition, but Ebstein and Grützner have met this view with the objection that the pepsin exists in greater quantity in the deep parts of the pyloric glands. These observers believe that it exists chiefly in the form of a pepsinogenic substance, as in order to extract it, it is necessary to add to the water hydrochloric acid or chloride of sodium.

Mucus secretion.—The gastric mucus, during the empty state of the viscus, usually forms a layer on the surface of the lining membrane. This mucus comes from the epithelial cells, which are found at intervals to have the appearance of goblet-cells, swelling up and discharging their contents.

The *circulation* in the coats of the stomach varies according to the phase of secretion: during fasting the mucous membrane is pale, with contracted blood-vessels, and the veins convey very dark blood; with the commencement of secretion the membrane is found to have assumed a rose-red color, with dilated vessels; the veins carrying blood of an almost arterial hue, while the whole membrane appears turgid, and perforated by numerous small openings which correspond to the tubular glands. The temperature at the same time increases by about 1°C. (1°·8 F.).

The *influence of the nervous system* is not well understood. There is no doubt that it is of reflex nature, and the starting point of the reflex may be either in the mucous membrane itself, or in some distant part, such as the buccal or lingual mucous membrane. The ganglia of Meissner's plexus are probably local reflex centres, which are in their turn influenced by the sympathetic ganglia, and more remotely by the cerebro-spinal axis. The course of the efferent nerve-fibres has not been traced. Cl. Bernard found that the secretion was arrested by galvanisation of the filaments which pass to the stomach from the semilunar ganglia. Extirpation of the *solar plexus* gave negative results in the hands of Budge, Schiff, Eckhard, &c. Braun found an increase of the secretion after section of the splanchnic nerves, but Schiff observed no result to follow.

ACTION OF THE GASTRIC JUICE ON FOOD.

The action of gastric juice is on the albuminoids of the food, which it converts into *peptones*. This change is one of bodies insoluble (or nearly so) and non-diffusible, into substances soluble and diffusible, and accordingly easily absorbed; so as to be ready to pass into the blood for the purposes of assimilation.

Peptones.—The following general characters distinguish peptones from ordinary albuminoids:—

(1) They are freely soluble in water;
 (2) They are highly diffusible; their endosmotic equivalent is very small.

(3) They are not precipitated by boiling;

(4) In dilute solutions they are not precipitated by nitric acid, acetic acid, or neutral salts.

(5) They are thrown down (in neutral or feebly acid solutions) by perchloride of mercury, nitrate of mercury, nitrate of silver, tannin, phosphomolybdic and phosphotungstic acids;

(6) The addition of a little soda, and one or two drops of a weak solution of sulphate of copper, gives a rose color to the solution (*reaction of Gorup-Besanez*).

(7) Dissolved in an excess of acetic acid, the solution gives, on addition of concentrated sulphuric acid, a violet-blue color, with a slight greenish fluorescence, and presents an absorption band between *b* and *F*. The result is more pronounced when chloride of sodium has been added (*reaction of Adamkiewicz*);

(8) Injected into the blood, they do not appear in the urine in the form of albumin. In the dry state peptones form transparent, amorphous substances, of a yellowish-white color, and hygroscopic nature. The characters of peptones are, however, found to vary with the mode of preparation, and the extreme difficulty of procuring them in a state of purity renders our notions of their composition and nature very uncertain.

According to Meissner there are three principal modifications: peptone, parapeptone, and metapeptone. The former substance, in its turn, presents three varying states:

(1) *Peptone A*: this is precipitated from neutral solution by concentrated nitric acid; and from solutions slightly acidulated with acetic acid by ferrocyanide of potassium.

(2) *Peptone B*: it is precipitated by ferrocyanide of potassium, and not by nitric acid.

(3) *Peptone C*: this form is not precipitated by either of the above reagents.

Para-peptone is precipitated from feebly acid or feebly alkaline solutions by a mixture of alcohol and ether; it is precipitated from acid solutions by concentrated solutions of the different neutral salts; prolonged exposure to the action of gastric juice or boiling makes it quite insoluble. This insoluble modification is called *dys-peptone*. The latter is probably not formed during normal digestion. Brücke and v. Wittich believe that para-peptone is subsequently changed into peptone, but Schiff does not think that this change takes place.

If the fluid has been exactly neutralised, and the para-peptone removed by filtration, the addition of a small quantity of acid (1:1000) gives a flocculent precipitate of *meta-peptone*, soluble in an excess of acid, and which reforms on the addition of a concentrated mineral acid.

According to some authorities, the peptones have nearly the same chemical composition as the mother substances from which they are derived, and the process of peptonisation consists merely in the relaxation of the molecular constituents. Adamkiewicz has found that peptones yield less ash than albumin, and remarks, in connection with this, the significant fact, observed by A. Schmidt, that ordinary albumin loses its property of coagulating by heat on removing a portion of its salts by diffusion.

According to Hoppe-Seyler, and some other authorities, however, the peptones represent the hydrates of the albuminoids from which they are derived.

The transformation of albuminoids into peptones is due to the action of pepsin, and the change takes place only in an acid medium.

Certain conditions favor this change; it is hastened by agitation and by a moderate temperature (36° — 38° C.; 96.8° — 100.4° F.). Diminution or elevation of the temperature slow the process, also the presence of an alkali, or an excess of acid. At 0° C (32° F.) the action is suspended for an indefinite period, but may be renewed by raising the temperature. Boiling destroys permanently the action of pepsin, and, accordingly, prevents the further change of albuminoids into peptone. The same result is produced by substances which precipitate pepsin, such as metallic salts, absolute alcohol, &c. The presence of an excess of peptones in the medium has also the effect of arresting the change.

Mode of action of the gastric juice. The nature of the part taken by the essential constituents of the gastric juice is not definitely known. According to Meissner, the liquid albuminoid constituents of the food cannot be digested till they are rendered insoluble in water, a change which requires the presence of an acid in excess. If this be not present, the soluble

albuminoids are not digested, but the insoluble are. The nature of the acid present has not an essential influence on the process of digestion; the proportional quantity present is of importance. For hydrochloric acid the proportion of .7 per 1000 gives the maximum results for the digestion of fibrin; 1.2 in case of digestion of albumin.

The pepsin is essential to the formation of peptones, and, as already seen, it can act only in an acid medium. The presence of a very small quantity of pepsin is sufficient to cause the change of a large quantity of albuminoids into peptone. Pepsin, accordingly, acts as a ferment, and is not destroyed during digestion. If the precaution be taken of removing the peptones by dialysis as soon as they are formed, and adding the necessary proportions of water and acid, the same quantity of pepsin will be found to digest almost unlimited quantities of fibrin. Schiff has, however, found that in using large quantities of fibrin, the digestion was definitely arrested at a certain stage for want of pepsin.

Action of gastric juice on the other aliments.—Some authorities, and among them Brown-Sequard, have admitted that gastric juice has the effect of changing starch into sugar, and Munk asserted that he had extracted a saccharifying ferment from the mucous membrane of the pig's stomach by the action of glycerine. Most authorities, however, deny this action. Harley has affirmed that the gastric secretion has the power of changing cane-sugar into grape-sugar, but it is still doubted by many observers.

The gastric juice dissolves gum and cane-sugar, without causing any change in their composition. It also dissolves the albuminous coats of the fat-cells, which has the effect of setting free the oil-globules which they contain. It has no action on elastic or horny tissue, nor on nuclein, mucin, or cellulose. The salts, which are soluble in acidulated solutions (carbonates and phosphates of lime, &c.) are dissolved. The carbonates are also changed into chlorides, and carbonic acid set free.

Autodigestion of the stomach.—Why it is that the coats of the stomach are not digested during life by their own secretion, is a question which has not yet been satisfactorily answered. Some have attributed the immunity of the mucous membrane to the presence of a layer of alkaline mucus which protects it from the gastric juice (Meissner). Others have attributed it to

neutralisation of the juice by the alkaline blood (Pavy). Cl. Bernard believed that the protection was due to the epithelium which was dissolved by the gastric juice, and as rapidly reformed. It has been supposed by Basslinger to be due to the tension of the tissues during life; but this idea is too mystic to be accepted as an explanation.

Pancreatic juice.

Pancreatic juice, as obtained from a temporary fistula in the dog, is a limpid, colorless fluid, without characteristic odor, and having a slightly saline taste. It is also viscid and ropy; flowing slowly from the canula by large pearly drops, and frothing when shaken. Its reaction is strongly alkaline (from the presence of carbonate of soda), and the specific gravity is 1.008—1.010. It contains usually no morphological constituents, although Kühne has described corpuscles, like the salivary corpuscles, with one to four nuclei. It is less ropy in the sheep, horse, ox and pig; while it is almost quite fluid in the rabbit. The daily quantity of pancreatic juice is, of course, very difficult to estimate, and different observers have obtained varying results. Colin has given the number of grammes per diem for each kilogramme of the weight of the animal: horse, 16.8; ox, 14.4; sheep, 12.0; pig, 7.2; dog, 2.4. By proportional calculation for man, it has estimated that the daily secretion would be 200—350 grammes. In a case of pancreatic fistula observed by Lacompte, in a female of seventy years, the daily quantity collected was from 80 to 125 grammes.

At a temperature of 75° C. (167° F.) pancreatic juice coagulates *en masse*; at 0° C. (32° F.) it forms a gelatinous mass, which liquefies on cooling. When left to stand, it loses its viscosity, becomes turbid, and readily decomposes. Treated with alcohol it gives a precipitate soluble in water; it is also precipitated by most of the concentrated mineral acids, by metallic solutions, by tannin, &c. The nitric acid precipitate soon changes to an orange-yellow. Acetic acid causes turbidity, which disappears on adding an excess. Chlorine water gives a white precipitate, which soon changes to a rose color; this tint disappears after a certain time, and may be restored by addition of nitric acid. According to Cl. Bernard this reaction does not appear when the juice is perfectly fresh.

This secretion contains about 10 parts per 100 of solid matters; of which 9 are formed by organic matters, and 1 by mineral salts. The proportion is, however, less in most animals than in the dog.

The fluid obtained from permanent fistulæ in animals is more watery and less alkaline than that obtained on opening the duct. It does not fairly represent the normal secretion, although Pawlow and Afanasiew think it does.

The pancreatic juice contains the following constituents:—

(1) *Albuminoids*—ordinary albumin and albuminate of potash.
 (2) *Ferments*—(a) one which changes albuminoids into peptone; (b) a second which saccharises starch; (c) a third which decomposes fats.

(3) *Leucin*. Traces of this substance are found in the fresh juice.

(4) *Soaps and fats* (traces of).

(5) *Salts*—Chloride of sodium (chiefly), phosphate of calcium, carbonate of sodium, with small quantities of chloride of potassium and phosphate of iron.

The pancreatic ferments present the following characters:—(1) The ferment which acts on the albuminoids (*trypsin* of Kühne, *pancreatin* of some writers), when isolated by the method of v. Wittich, forms a yellowish white powder, soluble in water, in glycerine, and in saline solutions; insoluble in alcohol. When dried, it can be heated to 110° C. (230° F.) without losing its activity. (2) The *diastatic ferment* appears to be identical with ptyalin. It diffuses more easily than the other ferments; it is precipitated from solution by alcohol, and partly by acetate of lead. In solution it loses its activity at 70° C. (158° F.), but, when dried, it may be heated to 100° C. (212° F.) without suffering any change. (3) The *ferment* which acts on fats has not been isolated.

The following analyses of the pancreatic juice of the dog are after Schmidt:—

	In 1,000 parts.	On opening the duct.	Permanent fistula.
Water	...	900.76	980.45
Solids	...	99.24	19.55
Pancreatin	...	90.44	22.71
Salts	...	8.80	6.84
Soda (united with the pancreatin)	...	.58	3.31
Chloride of sodium	...	7.35	2.50
Chloride of potassium	...	.02	.93
Phosphate of lime	...	.41	.07
Phosphate of magnesia	...	.12	.01
Phosphate of soda	...	—	.01
Lime (united with the pancreatin)	...	.32	—
Magnesia	...	—	.01

The secretion of pancreatic juice appears to be essentially intermittent; it commences immediately after the ingestion of food, and attains its maximum two hours after. It then gradually diminishes, and from five to seven hours after food the quantity increases to a second maximum (less elevated than the first), after which it quickly diminishes to a minimum, without its being possible to say that it ceases completely, till the next meal. (In the rabbit, whose intestines always contain food, it is not stopped, only diminished, during the intervals.) The secretion first poured out, after the commencement of digestion, is more viscid, of greater density, and easily coagulable; towards the end, it approaches the character of the fluid obtained from permanent fistulæ. The ingestion of rich food increases the quantity and improves the quality of pancreatic juice, which is deteriorated by anything that disturbs the general nutrition of the system.

Secretion of the pancreatic juices.—The physiology of this secretion resembles, in a great measure, that of the salivary glands. The *circulation* undergoes the same modifications as described in the case of the latter. The supply of nerves to this organ is very rich; the conditions of the nervous influences which act on it are not, however, well understood. The conditions of the secretion above-mentioned show that reflex stimulation from the mucous membrane of the stomach suffices to determine the activity of the gland, and the point of origin of the stimulus; for the second maximum is probably from the mucous membrane of the duodenum. The centripetal and centrifugal paths are, however, still unknown.

The *chemical composition* of the pancreas differs from most other glands: it contains, besides the ferments above mentioned, a considerable quantity of leucin, and of tyrosin; also small quantities of xanthin, hypoxanthin, guanin, lactic acid, and the fatty acids. Most of these are, however, probably due to decomposition; the pancreas decomposes very rapidly after death.

Stimulation of the medulla oblongata causes an increased secretion of pancreatic juice, but if kept up too long, diminution supervenes, and, finally, complete arrest of the secretion (Heidenhain). The same observer has found the secretion continue after section of the medulla, so that he does not believe that a secretory centre exists there. Lebediow has found similar results in case of the great splanchnic nerve: increase of the secretion by stimulation of the peripheral end; diminution if the stimulation be prolonged. Direct stimulation of the pancreas by induced currents causes an

increase of the secretion' (Kühne, Lea). Irritation of the central end of the pneumogastric nerve causes an *inhibitory arrest* of the secretion, and the same result is produced, according to Pawlow by irritation of any sensory nerves. Section of all the nerves which accompany the *arteria pancreatica magna* is followed by a profuse *paralytic secretion*, which is not arrested by stimulation of the pneumogastric.

The secretion is diminished or stopped by *atropin* (except in the rabbit); *physostigmin* increases it; *pilocarpin* or *nicotin* has no action. Landau has, however, observed an increase caused by the use of the latter. The action of curara is disputed; Bernstein has reported an increase, Heidenhain a diminution under its influence.

With regard to the formation of the active principles of the secretion, the researches of Heidenhain go to show that the trypsin is formed at the expense of another substance already existing in the cells of the acini. The cells have been divided by Heidenhain into two zones; an *internal zone*, granular, which does not stain with carmin; and a *peripheral zone*, homogeneous, containing no granulations, which stains readily with carmin. At the junction of these two (in the *median zone* of Langerhans) the nucleus is found. The granules of the inner zone disappear by the action of water, which disproves the idea of Langerhans, that they were fatty. During secretion the granular zone gradually diminishes in depth, having at first become more granular than before. The peripheral zone increases at the same time, and at the end of the secretion comes to occupy the whole of the diminished cell. Accordingly, when the gland is exhausted, the lining cells are much smaller, and the acini themselves shrunken; the granules have disappeared, except a few at the inner border of each cell. The central zone then increases, at the expense of the peripheral, during the interval of rest.

The glycerine extract of a perfectly fresh pancreas has no action on albuminoids; it does not contain trypsin, but it contains zymogen. The latter substance is changed into trypsin by the action of dilute acids, by water at a moderate heat, or by oxygen. The change is prevented by certain salts (chloride of sodium, or the alkaline carbonates). The proportion of zymogen present at any period corresponds to that of the granular contents of the cells. Accordingly, we are obliged to admit that the zymogen is changed into trypsin at the moment of secretion. Heidenhain attributes the change to the formation of an acid at the required moment; it has also been attributed to the influence of the increased amount of oxygen which is conveyed to the gland by the increased afflux of arterial blood.

Schiff and Herzen believe that the spleen has an essential influence in the formation of trypsin. The former has found that in animals from whom the spleen has been removed, the pancreatic juice has no action on albuminoids.

The pancreatic secretion is poured out at a low pressure, 16—17 mm. of mercury in the rabbit and sheep. Accordingly, the flow is easily retarded. It is not known whether resorption of the secretion causes any constitutional disturbance. But it is certain that it acts a local irritant, for ligature of the pancreatic duct is followed by cirrhotic changes in the gland; a chronic

inflammation resulting in hyperplasia of the interstitial connective tissue, and atrophy of the gland cells.

Action of the pancreatic juice on food.

The pancreatic juice acts on three varieties of food ; albuminous, saccharine, and fatty.

(1) *Albuminoids*.—The pancreatic juice converts albuminoids into peptone. This action was first demonstrated by Bernard and Corvisart, and is now universally admitted. The change takes place in a way that distinguishes it completely from the similar effect produced by the gastric juice. The digestion of albuminoids by the pancreatic juice may be divided into three stages :—

(1) The first is the change of albuminoids into peptone. This transformation is very energetic, and takes place whether the medium be alkaline, neutral, or feebly acid. It is not preceded by any swelling, and the resulting peptones appear to be identical with those obtained by the action of the gastric juice. They are somewhat richer, however, in carbon and oxygen than the gastric peptones.

Like the gastric digestion of albuminoids, this change is promoted by moderate heat, but it differs from the former in not being arrested by accumulation of peptones. It is favored by the presence of certain salts : carbonates of sodium (.9—1.2 per cent.), of potassium, of ammonium, also by chloride of sodium, or of ammonium, sulphate of sodium, nitrate of potassium ; the presence of bile or biliary salts also promotes the change (contrary to what holds good in case of the gastric digestion of albuminoids). It is also promoted by free access of oxygen, although the change will take place in an atmosphere of pure hydrogen (Hüffner). Also, the presence of large quantities of carbonate or chloride of sodium, or addition of beer yeast. Cl. Bernard believed that the action of the pancreatic juice required the previous influence of the gastric juice and bile, but Corvisart has shown that this secretion alone is able to digest albuminoids.

(2) The primary stage is followed by another, in which large quantities of leucin and tyrosin are formed ; these are produced at the expense of the peptones already formed.

With the leucin and tyrosin other products are formed : asparagic and glutamic acids, and glycocoll. According to Kühne, these various substances are formed at the expense of one portion of the peptone (about half) ; to this part he gives the name of *hemipeptone*, while he has applied the term *antipeptone* to the part of the peptones which undergoes no alteration.

(3) In the third stage a diminution takes place, not only of the peptones but of the leucin and tyrosin, and a number of new substances are formed, which give rise to the characteristic faecal odor; indol, phenol, volatile fatty acids, a substance which is precipitated by chlorine water in the form of violet filaments, &c.; while a number of gases are disengaged at the same time, hydrogen, nitrogen, carbonic acid, sulphuretted hydrogen, carburetted hydrogen. This last stage progresses with greater rapidity in an alkaline medium; it is retarded by a very slight degree of acidity.

Pancreatic juice has no action on nuclein, keratin, amyloid substance, or on connective tissue fibrils; elastic tissue, on the other hand, is digested.

Why the pancreatic juice does not digest the walls of the intestine, or of the gland-ducts, or the margins of the fistula in case of an artificial opening, is a question which still remains unanswered.

Action on amylaceous food.—This action is identical with that of ptyalin (Valentin, Bouchardat, Sandras), but is more rapid; at a temperature of 37° — 40° ($98^{\circ}.6$ — 104° F.) it is almost instantaneous. The achroodextrin of Brucke, which resists the action of ptyalin, is also converted into grape-sugar by the pancreatic juice.

Action on fats.—The action of pancreatic juice on fats is two-fold: (1) It *emulsifies* them; if fats be shaken up with pancreatic juice, a white emulsion is formed, in which the fat globules are still more finely divided than in milk (Cl. Bernard). It requires about double the quantity of this secretion to emulsify a certain quantity of fat. (2) It *decomposes fats into fatty acids and glycerine*. The fats so liberated unite with the soda of the pancreatic juice and bile to form soaps.

Bile.

Bile is secreted by the liver, of which we have already described the minute structure. In man it is a neutral or feebly alkaline fluid, of an orange-yellow or golden color; clear, inodorous, with an excessively bitter taste, followed by a sweetish, nauseous after-taste. When it has remained some time in the gall-bladder, it assumes a greenish color, and develops a characteristic odor; at the same time it becomes

viscid and ropy from the addition of mucus. Its specific gravity is from 1.026—1.030. Exposed to the air, it becomes acid, and crystals of cholesterin are precipitated, while fatty acids are set free.

Pure bile is not coagulated by heat; that of the gall-bladder gives a precipitate with alcohol and with acetic acid (mucin). The addition of sulphuric acid makes it fluorescent; it gives a deep red with transmitted, green with reflected, light.

Chemical composition.—Bile contains 1.2—2.28 parts per 100 of solid matters. It contains, besides water, the following constituents:—

- (1) Two characteristic biliary acids, *glycocholic* and *taurocholic*, in the state of glycocholate and taurocholate of sodium;
- (2) Coloring matters: *bilirubin* and *biliverdin*;
- (3) *Cholesterin*;
- (4) *Mucin*;
- (5) Traces of nitrogenous compounds: lecithin, urea, &c.
- (6) Non-nitrogenous substances: fats, soaps, alkaline palmitates, and oleates;
- (7) A diastatic ferment.
- (8) Inorganic salts: iron (in considerable quantity); traces of manganese, and copper (sometimes).

The *quantity* of bile is proportionally greater in the herbivora than in the carnivora. It is impossible to make a perfectly accurate estimate of the daily amount (about 1 kilogramme in man), but the following figures give the results of careful observation. The numbers are the grammes in 24 hours per kilogramme of the weight of the body:—

Man	.	.	14 grammes.
Cat	.	.	14 "
Dog	.	.	20—60 " grammes.
Calf	.	.	25 "
Rabbit	.	.	132 "

The biliary secretion is continuous, but it increases during the time of digestion. In man it attains a maximum in four to eight hours after ingestion of food. The exact time of the maximum has been disputed: Arnold and Voit place it soon after taking food; Bidder and Schmidt between the third and fifth hour, while Kölliker and Muller saw a second maximum (in case of a very large meal) about 14—16 hours after.

The following tables give the mean of several analyses of human bile :—

In 1000 parts.	Trifanowski.	Socoloff.	Hoppe-Seyler.	Jacobsen.
Water . . .	910.70	—	—	—
Solids . . .	89.21	—	—	—
Glycocholate of sodium . . .	4.37	—	30.3	44.8
Taurocholate of sodium . . .	19.25	15.67	8.7	—
Taurocholate of sulphur . . .	—	.92	.516	—
Salts of the biliary acids . . .	23.62	64.71	—	.44
Fats . . .	3.59	—	7.3	6.4
Soaps . . .	16.32	14.58	13.9	9.42
Cholesterin . . .	3.35	—	3.5	.21
Lecithin . . .	.17	—	5.3	—
Mucin . . .	12.98	} 37.24	12.9	} 10.0
Other inorganic substances, insoluble in alcohol . . .	14.59		1.4	

The *sulphur* which is found in human bile comes from the taurocholates. The dried residue of the alcoholic extract of human bile contains, in 100 parts, 1.46 parts of sulphur (Bensch). *Iron* is always present; Hoppe-Seyler has found the average proportion .062 per 1000.

Secretion of Bile.

The mechanism of the biliary secretion is still very obscure. Of the two vessels which convey blood to the organ, vena portæ and hepatic artery, the proportional diameters are as 5 : 1. The artery supplies Glisson's capsule, the walls of the bile canals, and sends lobular capillaries to be distributed in the intermediate zone of each hepatic lobule. It should be mentioned that this particular arrangement, already mentioned, and described by Virchow and Chrzonszczewsky, is denied by Cohnheim and Litten. It is essentially the nutrient artery of the gland, and deligation has been followed by gangrene of the hepatic tissue.

The vena portæ is distributed to the lobules only. Ligature of this vessel has been followed by suppression of the biliary secretion, accompanied by the development of symptoms of narcotism, stupor, and coma, soon followed by death. Slow obliteration, on the other hand, does not cause suppression of bile; it is only less abundant and less watery (Moos), and cases of pathological obliteration in man have been reported by Andral and by Gintrac, in which the secretion persisted.

The influence of the hepatic artery has also been disputed. Ligature of this vessel in the rabbit has been followed by arrest of the secretion

(Kottmeier) ; by slight diminution (Röhrig) ; by no change of its quantity (Schiff, Betz).

The influence of innervation on the secretion is not well known. Destruction of the nerve entering the liver with the arteries has given no result (Picard). Stimulation of the medulla has been found to cause a diminution of the secretion (Lichtheim, Heidenhain) ; this is preceded by a slight increase, which is referred by Heidenhain to contraction of the bile-ducts, while the same observer refers the decrease to vascular contraction causing a lowering of the vascular pressure. The vaso-motor fibres pass along the splanchnics (Munk) : stimulation of the splanchnics is followed by the same result as that of the medulla, and after section of these nerves stimulation of the medulla has no effect.

Biliary acids.—There can be no doubt that the biliary acids are formed in the liver, although their source and mode of production are obscure. In the normal state their existence has been made out only in the liver and bile, and they do not accumulate in the blood after extirpation of the gland (Kunde, Moleschott). Naunyn asserts that they exist in normal urine, but even if this were the case they should come obviously from the bile.

Bilirubin.—This is the coloring matter of human bile, and of that of carnivorous animals, and is undoubtedly derived from the hæmoglobin. It is probably formed for the most part, if not entirely, in the liver ; but there is reason to believe that it may be formed elsewhere, in exceptional circumstances.

Cholesterin.—The hypothesis of Flint, which makes this compound to be derived from the disassimilation of nerve tissue, is not generally accepted. There seems to be an intimate relation between it and the biliary acids, and it has been found in many tissues and organs besides the nervous ; hæmoglobin contains about 2.5 per 1000, according to Hoppe-Seyler.

The influence of different substances on the biliary secretion has been studied with great care, especially by Rutherford. The following markedly increase its quantity : nitro-hydrochloric acid, phosphates of sodium and of ammonium, phosphate of potassium, podophyllin, aloes, colocynth, ipecacuanha, colchicum, benzoate of soda, salicylate of soda. A less energetic influence is exerted by rhubarb, jalap, sulphate of sodium, &c. ; and a feebler action still by senna, scammony, croton oil, chloride of sodium, and jaborandi. No effect was produced by calomel, or by sulphate of magnesia ; only one substance, acetate of lead, was found to *diminish* the secretion.

During the intervals of digestion, the bile accumulates in the gall-bladder. The continuous formation in the hepatic lobules is followed by displacement of the fluid already in the ducts. The progression of the fluid is promoted by the contractile walls of the ducts, and also by the inspiratory movements. At the time of digestion the gall-bladder is emptied of its contents, partly by the contractions of its own muscular walls, and partly by the external pressure exercised by the increase of volume of the surrounding organs (stomach,

liver, duodenum). This increase is partly due to the physiological congestion which exists during digestion, and partly to mechanical distension, produced by the introduction of food. The pressure in the bile-ducts also increases during digestion, as the secretion is formed in greater quantity.

Action of bile on the different kinds of food.—(1) *Albuminoids.* On this class of foods bile has no digestive action. It precipitates from solution in dilute acids and gastric juice. The peptones and the parapeptones produced in the gastric digestion of albuminoids give, with bile, a yellowish, flocculent, somewhat resinoid precipitate, which adheres to the villi, and is easily recognised. This consists of biliary acids and pigments, and also a certain proportion of albuminoid matters. The pepsin of the gastric juice is carried down with this precipitate.

(2) *Hydrocarbons.*—Most observers have denied that bile has any action on starchy food, but V. Wittich has obtained from fresh bile a ferment which converts starch into glucose, and his results have been confirmed by Gianuzzi and Bufalini.

(3) *Fats.*—Bile emulsifies fats, but much less completely than does the pancreatic juice. But when the fatty acids have been set free by the action of the latter secretion, they combine with the alkalies of the bile to form soaps, and the biliary acids are set free. The resulting mixture of soaps and biliary acids promotes the emulsification much more rapidly than would the bile alone.

Uses of bile.—The part taken by this secretion in the digestive function is still undetermined. According to some, it aids in the digestion of fats, in the way above mentioned. It has also been supposed that by precipitating the peptones it ensures their complete absorption. Others believe that its action is entirely *post-digestive*, and is manifested in promoting the absorption of fats by its peculiar power of increasing the permeability to oils of any animal membrane moistened with it. Schiff believes that its action commences when the chyle has entered the villi, and consists in stimulation of the smooth muscular fibres, by the contraction of which the chyle is pressed into the subjacent lymphatics. The relaxation of the muscular fibres would be followed by a determination of the fatty particles towards the empty lacteal in the centre, and by this a continuous pumping action of the villus is kept up.

Bile also stimulates the peristaltic contractions of the intes-

tinal wall (*nature's purge*), and the introduction of a large quantity into the alimentary canal is followed by vomiting and diarrhoea.

It prevents putrefaction of the contents of the intestine, and in dogs with biliary fistulæ, the use of a meat diet causes excessive formation of gas, while the stools are of extreme foetor. According to Stolnikoff, however, bile has no anti-putrescent action, and this result is produced by causing rapid absorption of fermentable substances.

Intestinal Juice.

The intestinal juice (*succus intestinalis*, *s. entericus*) is secreted by Lieberkühn's glands. Obtained from the small intestine by Thiry's method, it is a transparent, limpid fluid, with a slightly yellowish tint. It has an aromatic odor, and highly alkaline reaction. Its specific gravity is 1.0115; it effervesces with acids, and coagulates by heat. It contains 2.5 per 100 of solids (albumin, organic matters of undetermined nature, and salts, especially carbonate of soda). It sometimes contains yellowish flocculi, due to agglomerations of mucus corpuscles (Mosloff). According to Claude Bernard it contains a ferment (*ferment inversif*), which converts cane-sugar into inverted sugar, a mixture of glucose and lævulose.

Thiry has obtained a maximum quantity of four grammes per hour from an intestinal surface of thirty square centimetres. The secretion does not appear to be continuous, but goes on, *pari passu*, with the digestive changes in the intestine. It is brought on by the presence of aliments, or by any kind of mechanical irritation, also by chemical stimuli, or by the use of electricity. The introduction of neutral salts, or of calomel, into the intestine also promotes the secretion. Iodine, bromine, sulphocyanides, &c., when introduced into the system, appear in the intestinal secretion. Iron, or arsenic, does not appear.

The secretion obtained from the large intestine has nearly the same characters: it is somewhat viscid, slightly turbid, and possesses a strongly alkaline reaction. No ferment has been found to exist.

The secretion obtained from Brunner's glands has not been isolated in a state of purity. It appears to be more viscid than the secretion of the rest of the intestinal tract, and is also

strongly alkaline. According to Grützner it is identical with the pyloric secretion of the stomach, and contains pepsin.

The following is an analysis (after Thiry) of the intestinal juice of the dog —

Water	.	.	975.861
Albuminoids	.	.	8.013
Other organic matters	.	.	7.737
Salts	.	.	8.789

Besides the above secretions, the intestine always contains a certain quantity of alkaline mucus, which comes from the epithelial cells. Hoppe-Seyler even questions the existence of any secretion of the intestinal glands, but mucus only.

With regard to the influence of the *nervous system*, it has been found that section of the nerves of a loop of intestine is followed by a copious flow of a watery, alkaline fluid (*paralytic juice*; Moreau, Kadziewski). Extirpation of the semilunar ganglia and solar plexus has been followed by the same result (Budge, Samuel), but negative results have been obtained by Adrian, Ramanski, and Radziejewski.

Action of the intestinal juice on food.—The influence of this secretion on food has been greatly controverted, and still remains unsettled. According to Leven, an infusion of the intestinal mucous membrane digests albuminoids, emulsifies fats, and converts cane-sugar into glucose; in fact, it supplements all the actions of the pancreas, and the experiments of Busche (in case of a woman with duodenal fistula) tend to confirm this view, except with regard to the action on fats.

(1) *Albuminoids.*—In addition to the views just mentioned, we may mention that Schiff has found digestion of albuminoids effected by the intestinal juice (obtained by Thiry's method), while the researches of Lehmann, Braune, and Funke have given negative results. Lander, Kölliker, and Müller have found that fibrin and other albuminoids were digested by the juice of the cat and dog, while Funke and Frerichs have obtained contrary results in case of the rabbit, indicating a probable difference in the secretion of carnivorous and of herbivorous animals.

(2) *Hydrocarbons.*—The action on starch appears to be better established than that on albuminoids, although the fluid obtained by Thiry's method has certainly no saccharising power. It has been shown by many observers in case of the lower animals, and demonstrated by Busch in the case of duodenal fistula, already referred to. The inversive ferment of Bernard has been mentioned already.

(3) The action on *fats* remains doubtful. According to R. Demant, emulsion is produced only where free fatty acids are present, not otherwise. The secretion of the large intestine appears to have no action on food. Some observers have, however, attributed to it a saccharising power.

Paladino affirms that the *æcal juice* of the large herbivora has this action, but only for certain substances, such as oats.

With regard to the secretion of Brunner's glands, the view of Grutzner has been mentioned above. Costa and Krolow have attributed to it the power of changing starch into glucose, but nobody has succeeded in obtaining a diastatic ferment from it.

DIGESTION IN THE DIFFERENT STAGES OF THE ALIMENTARY CANAL.

The changes which the food undergoes in the various parts of the digestive tube will have been gathered from the account of the different influences to which it is subjected.

In the buccal cavity.—The trituration to which the food is subjected in the mouth converts the hard morsel into a soft mass, which is easily adapted to the form of any part of the tube which it has to traverse, and is rapidly permeated by the various digestive juices. Accordingly the duration of the process of mastication varies with the nature of the aliments used, and want of teeth seriously interferes with the digestive process, as is seen in edentulous old people. The chemical changes which the food undergoes in the mouth, have been described in studying the properties of the saliva. It must be remembered, however, that the stay of the food in the mouth is so short that those changes are merely initiated here, but they continue in the sub-diaphragmatic parts of the alimentary canal. The passage through the *pharynx* and *œsophagus* is too rapid for the food to undergo any notable changes in the transit.

In the stomach.—The arrival of the first masses of food in the stomach, causes an immediate turgescence of the mucous membrane, and a copious flow of the gastric juice, which continues during the time the aliments remain in the stomach. Gastric digestion is characterised by the change of albuminoids into peptone, but even in the stomach the delay of the aliments is not sufficiently long to allow more than the initiation of this transformation, which is completed in the small intestine. Indeed, some authors (especially Leven) have gone so far as to deny all digestive action to the stomach, regarding its function as purely mechanical, and preparatory to the changes of solution and disassociation which the aliments undergo in the intestine.

The mixed contents of the stomach after subjection to the gastric juice, form the fluid known as *chyme*. The chyme comprehends the following :—

Substances which resist digestion : cellulose, elastic tissue, horny tissue, &c. ;

Aliments not yet digested : albuminoids, hydrocarbons, fats, &c.

Broths ;

Salts ;

Aliments partly digested (partly modified by the action of the saliva and gastric juice) ;

Glucose, and, under certain conditions, lactic and butyric acids,

Peptones (traces of) ; the quantity is always very small, for they are absorbed as quickly as formed ;

Saliva and gastric juice :

Epithelial debris ;

The stomach also contains a small amount of gas, which increases under certain conditions. A part of this comes from the air which is swallowed with the food, and a part from decomposition of the aliments. The stomach is the seat of a true respiratory process on a rudimentary scale ; the oxygen swallowed with the food is partly absorbed by the mucous membrane, and carbonic acid is exhaled. The whole of the carbonic acid is not, however, derived from this source ; a part comes from the carbonates which are decomposed by the gastric juice, and possibly from the butyric fermentation. Chevreul has found hydrogen in the stomach of an executed criminal. The following analyses of the gases of the stomach are given on the authority of Planer :—

CO ₂	per 100 vols	(I.) 20.79	(II.) 33.83
H	„	6.71	27.58
N	„	72.50	38.22
O	„	..	.37

The time which the aliments pass in the stomach is very variable ; liquids spend but a very short time ; in a case of duodenal fistula, pure non-coagulated milk was seen to appear at the orifice a few minutes after swallowing, and has been supposed to pass along the lesser curvature to the pyloric orifice without mixing with the contents of the

stomach. Of the solids, small pieces appear in the duodenum in about fifteen or twenty minutes after deglutition, and continue to pass through for some hours; in general, at the end of four or five hours, gastric digestion is complete, and the stomach empty.

The emptying of the stomach takes place in two ways: (1) by absorption of the peptones; (2) by the passage of the chyme into the duodenum. Richet differs from other physiologists in his account of the passage of the chyme into the duodenum, as he affirms from his observations on Marcelin that the gastric contents pass through the pylorus *en bloc*, the transit not occupying more than a quarter of an hour.

In the small intestine.—Once arrived in the small intestine, the acid chyme causes a copious flow of bile, pancreatic juice, and intestinal juice, while the gastric juice ceases to have any digestive action. According to Schiff, the neutralisation of the acid mixture is effected chiefly by the secretion of Brunner's glands.

All the constituents of food are modified, and prepared for absorption by the secretions which are poured into the small intestine. The resulting mixed fluid is called *chyle*. It differs from chyme by its alkalinity, the smaller proportion of non-digested aliments present, in the existence of traces of leucin and of tyrosin, and the presence of the intestinal secretions, especially bile.

The *gases* of the small intestine consist of nitrogen, carbonic acid, and hydrogen. It contains but traces of oxygen. The hydrogen and a part of the carbonic acid come from the butyric fermentation of the hydrocarbons. The remainder of the latter gas is derived from the blood, as in the stomach; and, according to Strassburg, it is formed in the intestinal glands. The following table gives five analyses of the gases of the small intestine of man. The first three are by Chevreul (from the bodies of criminals); the two last are by Planer:—

		(34 yrs. old.)	(25 yrs.)	(23 yrs.)		
CO ₂	..	24.4	40.0	25.0	16.23	32.27
H	..	55.5	51.1	8.4	4.04	35.55
N	..	20.1	8.9	66.6	79.73	31.63
O	..	—	—	—	—	.05(?)

The time occupied by the aliments in their descent along

the small intestine is difficult to determine. Braune, in a case of artificial anus, situated 24 centimetres above the ileo-cæcal valve, found that the liquid portions of food appeared at the fistula about 3 hours after food, while the last portions arrived in 5—6 hours. These observations have been confirmed by Lossnitzer in a similar case.

In the large intestine.—Although the secretion of the large intestine is an alkaline fluid, the contents of this part of the tube are always acid. This acidity is due to decomposition (decomposition of the fats by the pancreatic juice, butyric and lactic fermentation of the hydrocarbons, &c.).

The bile is gradually decomposed, giving rise to the formation of taurin, glycoll, cholalic acid, choloidic acid, dyslysin, and urobilin. The changes of the pancreatic and intestinal juices are not known.

Characters of the excrements.—The color of the fæces depends chiefly on the bile, as is shown by their paleness in cases where the bile is absent. Still the color of the food has a considerable influence; when exclusively animal, the fæces are dark in color; a mixture of saccharine food and meat gives a yellowish-brown; a fresh vegetable diet gives a green tinge.

The *consistence* is various, and depends chiefly on the rapidity with which they have traversed the large intestine. When this takes place slowly, the liquid parts become absorbed, and the remaining mass has a somewhat solid consistence. The *specific gravity* is less than that of water.

The *reaction* is generally acid, especially after amylaceous food, still the reaction is sometimes neutral or slightly alkaline (ammoniacal fermentation).

The *quantity* varies between 60 and 200 grammes, but may go up to 400 or 500 grammes, especially with the use of vegetable food.

The following substances are present :—

(1) The indigestible parts of the food : elastic tissue, horny tissue, mucin, nuclein, cellulose, chlorophyll, insoluble salts (salts of lime, soaps of lime, &c.) ;

(2) Undigested portions of food which have been incompletely or not at all affected by the digestive juices ;

(3) Epithelium of intestine ; intestinal mucus.

(4) Biliary constituents more or less decomposed : coloring matters of bile and urobilin ; biliary acids (especially glyco-

cholic, which decomposes with difficulty), cholalic acid, taurin, dyslysin (Hoppe-Seyler doubts this) ; cholesterin (according to Flint it is a product of decomposition of cholesterin, *stercorin*) ; lecithin ;

(5) Products of decomposition ; volatile fatty acids (acetic, butyric, caproic, isobutyric, valeric) ; palmitic and stearic acids ; oleic acid ; lactic acid ; phenol, indol, scatol, excretin ;

(6) Salts, soluble and insoluble ; chlorides, phosphates and alkaline sulphates ; phosphates of chalk and of magnesia ammonia-magnesian phosphate ;

(7) Germs of inferior organisms (bacteria, vibriones) ;

The following analyses of human *fæces* are from Berzelius and Wehsarg respectively :—

Water	..	..	753.	..	733.
Solids	..	..	247.	..	267.
Biliary salts	..	..	9.	..	—
Mucus and biliary resin	..	..	140.	..	—
Albuminoids	..	..	9.	..	—
Extractive matters	..	..	57.	..	—
Aqueous extract	..	..	—	..	53.40
Alcoholic extract	..	..	—	..	41.65
Ethereal extract	..	..	—	..	30.70
Residue of food	..	..	70.	..	83.
Salts	..	..	12.	..	—
Earthy phosphates	..	..	—	..	10.95

Gases of the large intestine.—The gases found in the large intestine are made up of carbonic acid, nitrogen, hydrogen, and marsh gas ; traces of sulphuretted hydrogen are found. Oxygen or ammonia is not present. These gases come partly from the air swallowed with the food, partly by exhalation from the intestinal mucous membrane, partly from chemical changes of the contents of the intestine. When an animal diet is used, there is an abundance of nitrogen, but little carbonic acid or hydrogen ; a milk diet gives much hydrogen, and little or no marsh gas ; legumes produce a large quantity of marsh gas, and little hydrogen. No gases are found in the intestine of the *fœtus*.

MOVEMENTS OF THE ALIMENTARY CANAL.

Deglutition.—The act of deglutition—by which the masticated bolus is conveyed to the stomach—is usually divided

into three stages : in the first it clears the isthmus faucium : in the second it passes through the pharynx ; in the third it descends through the œsophagus and passes into the stomach.

(1) The bolus having been prepared by the previous mastication and impregnation with saliva, is gradually carried backwards by the pressure of the tongue against the palatine arch. So long as the bolus is retained within the oral cavity, its movements are completely under our control, but as soon as it reaches the anterior pillars of the fauces, an involuntary reflex movement is initiated which it is impossible to arrest. At the commencement of the first stage, the tongue is raised by the action of the stylo-glossi, and pushed up from below by the mylo-hyoid muscles ; at the same time the intrinsic fibres by their contraction press the bolus from before backwards against the palatine arch and velum, which is made tense by its own circumflex muscles, and by the palato-glossi. As soon as the bolus has passed the anterior pillars, the contraction of the latter muscles causes them to meet in the middle line, shutting off completely the buccal cavity from the pharynx, and so completing the first stage of deglutition.

(2) The second stage possesses great mechanical as well as physiological interest, and, in addition to the movements of the pharyngeal walls by which the bolus is propelled downwards, the occlusion of three passages is necessary—the nasal fossæ, the larynx, and the isthmus faucium.

(a) *Movements of pharynx.*—These are of two kinds, *elevation and contraction* :—(1) The middle and lower parts of the pharynx are raised, and this movement is accompanied by a simultaneous elevation of the larynx, as can be ascertained by placing the finger on the pomum Adami during the act of swallowing. The previous fixation of the lower jaw is necessary for this movement, and on this account swallowing cannot be effected with the mouth open, except some hard body is placed between the teeth to give a point of resistance. The elevation of the pharynx is then effected by the palato- and stylo-pharyngeus muscles, with the upper fibres of the constrictors, aided by the supra-hyoid muscles, which by drawing forward the larynx and middle constrictors tend to open the post-oral part of the pharyngeal cavity for the reception of the bolus. (2) As soon as the bolus has passed into the pharynx-

geal cavity the constrictors contract in order, from above downwards, so as to press the bolus into the œsophagus, and the whole action of the pharynx is obviously related to the peristaltic action of the intestinal walls.

(b) *Occlusion of the isthmus faucium*.—This has been already described at sufficient length.

(c) *Occlusion of the posterior nares*.—This, is effected by the action of two set of muscles: (1) the levator and tensor palati of each side raise and stretch the soft palate, while (2) the palato-pharyngei muscles in the posterior pillars of the fauces contract and meet in the middle line behind. The uvula fills up the intervening chink (if any remain), and in this way a complete septum is formed between the nasal and buccal segments of the pharyngeal cavity.

(d) *Occlusion of the glottis*.—During this stage of swallowing the tongue is drawn upwards and backwards, while the hyoid bone (with the attached larynx) is jerked upwards and forwards, a double movement which results in the complete covering of the glottis by the base of the tongue. The aryteno-epiglottidæan folds are approximated by the contraction of their own fibres, and meet in the middle line, while the valve-like epiglottis which, pushed down mechanically by the base of the tongue, acts as an additional safeguard. But the opening is so well guarded that, even after extirpation of the epiglottis, deglutition of solids is not at all impaired, and that of liquids is but slightly affected, the last few drops appearing to trickle into the larynx (Longet, Schiff). If the parts be examined after swallowing a bolus stained with ink, the posterior surface of the epiglottis and the interior of the larynx are found to be completely unstained, while the base of the tongue, glosso-epiglottic folds, laryngo-pharyngeal gutters, &c., are all colored (Guinier). After ulcerative destruction of the epiglottis (in phthisis or syphilis), deglutition is but little impaired.

The closing of the glottis does not appear to be essential to safe deglutition, for Longet tracheotomised animals, and introducing a forceps through the wound, kept open the glottis without impairing the deglutition of solids or liquids. This observer had also an idea that the occlusion of the glottis is due to the action of the inferior constrictor, and not to that of its proper muscles.

(3) The ascent of the larynx opens the upper part of the œsophagus to receive the descending bolus (Guinier, Arloing). The descent is hastened by the vermicular contraction of the œsophageal walls, which is conducted on the most favorable mechanical principles. The longitudinal fibres, contracting, tend to draw the wall of the tubes past its contents; while the circular fibres, contracting behind, press the latter onwards. The influence of gravity is of no importance; animals swallow against gravity, and jugglers exhibit the feat of drinking a glass of wine up the throat instead of down.

The bolus is carried down with great force; in Mosso's experiments on the dog he found it was carried against a weight of 450 grammes attached to it. To ascertain the time occupied by the bolus in its descent Hamberger made use of the stethoscope. He found it to occupy a distinctly appreciable period of time, which also varied considerably with the state of the nervous system, of the general health, &c. According to Ranvier it is always arrested for a moment just before passing the cardiac orifice of the stomach (Ranvier's *fourth stage of deglutition*).

For the performance of the act of deglutition there must be something to swallow; the reflex movements of the act cannot be effected without the application of a stimulus to the mucous surface. There are, however, restrictions to this statement if, as Mosso and Magendie have affirmed, we can swallow air alone. According to Schiff, in the swallowing of liquids, some drops are always left in the glosso-epiglottic groove, which give rise to a *secondary deglutition*. This is, he believes, determined by the irritation of the mucous membrane of the larynx, produced by the trickling of the fluid into its interior.

The *nervous mechanism* of the act of deglutition is very complicated. The presiding centre is in the medulla oblongata. Afferent impulses are conveyed to this centre from the region of the fauces by the glosso-pharyngeal, superior laryngeal (tongue and pharynx, glottis), and some branches of the tri-facial (velum). Stimulation of any of these nerves produces movements of deglutition (Waller, Prevost). The sensibility of the œsophagus comes from the vagus. The afferent impulses descend the hypoglossal to the muscles of the tongue, the facial to the muscles of the palate, the glosso-pharyngeal and vagus (pharyngeal plexus) to the muscles of the

pharynx, the trigeminal to the supra-hyoid muscles, and the inferior laryngeal to the muscles of the larynx.

Movements of the Stomach.

These movements have been observed in the human being in some cases of gastric fistula, and in animals by freely opening the abdomen. Rhythmic waves of contraction are seen to pass from the cardiac end of the stomach towards the pylorus, but the spontaneous contractions of its walls are seldom very well pronounced. Local galvanisation produces an annular contraction at the part irritated. According to the observations of Beaumont, the gastric contents always pass in a definite current along the great curvature to the pylorus, whence they return along the lesser curvature to the cardiac end, from which the same course is re-commenced. This rotation occupies from one to three minutes. Brinton, on the other hand, asserted that the direction of the currents formed by the gastric contents is that indicated in the figure.



Fig. 56.

The stomach, when empty, presents anterior and posterior surfaces, looking backwards and forwards; but as it becomes gradually distended by the introduction of food the great curvature and cardiac cul-de-sac are turned forwards to the anterior abdominal wall. At the same time the contractions of the gastric walls, although not powerful, are sufficient to mix up the food with the gastric juice. Sir E. Home found in the stomach of

a recently-executed criminal a contracted muscular band dividing the cavity into two bags (*Home's hour-glass constriction*). He believed, but, of course, unjustly, that of these two the cardiac was for maceration of food, the gastric for digestion proper. In recent years Küss has called attention to the constricting band of oblique fibres (*cravate de Suissor*), which, by its contraction, divides the stomach during digestion into two parts: a left-inferior, corresponding to the great cul-de-sac, and a right-superior, which rather forms an elongated canal. The former retains the more solid aliments till fully acted on by the gastric juice, while the superior passage allows fluids to pass along the lesser curvature into the duodenum. This phenomenon has been observed directly by Larcher in the stomach of a dog during digestion. In the early period of gastric digestion the pyloric orifice is tightly closed by the contraction of its sphincter, which momentarily relaxes from time to time to allow a small portion of the fluid chyme to pass into the duodenum. As digestion progresses these relaxations are more frequent and last a longer time, and at last the exhausted sphincter yields completely, and allows the contents of the stomach to pass whether digested or not.

In order to study the movements of the stomach and the direction of the currents within its cavity, Reclam has adopted the plan of giving dogs a large quantity of milk rich in casein. On destroying the animals during digestion the grooves on the surface of the coagulated mass will be found to indicate the direction of the fluid currents.

Vomiting.—The act of vomiting is usually preceded by a peculiar sensation, that of nausea (*vau*, a ship). The mechanism of the act has been studied with great care by Schiff, who divides it into two stages (*stade préparatoire, stade d'expulsion*). The *preparatory* stage consists of the *active* dilatation of the cardiac orifice, which can easily be felt by passing a finger through a gastric fistula into the cardia, and is effected, according to Schiff, by the contraction of the oblique fibres of the œsophagus; for if these fibres are crushed by application of a ligature a little below the cardiac orifice, vomiting is no longer possible. The *stage of expulsion* calls in the aid of the abdominal muscles and diaphragm, by whose pressure the gastric contents are squeezed out through the open cardiac orifice, while the tight closure of the pyloric sphincter prevents the passage of any into the duodenum. Accordingly, when the

abdominal cavity is laid open, vomiting becomes very difficult, and is incompletely performed ; while the action of the abdominal muscles is sufficient to effect it, after the substitution of a pig's bladder for the stomach, when tartar emetic is injected into the veins (Magendie's experiment). The elevation of the cardia is necessary (Tantini) ; this gives a fixed point, from which the longitudinal fibres of the œsophagus contract, and on this account animals, in whose bodies the cardia is far below the diaphragm, vomit with great difficulty or not at all. The occlusion of the glottis and posterior nares is effected as in swallowing, and the instinctive stretching of the neck, which is done during the act, facilitates the passage of the gastric contents upwards by tending to straighten the passage.

Eructation is the sudden expulsion of gas from the stomach, with the production of a sound at the upper end of the œsophagus.

Regurgitation consists of the return of food from the stomach into the mouth, unaccompanied by voluntary effort. In some cases the food can be brought up at will, and the act becomes habitual (*rumination, merycism*).

Innervation —The nervous supply of the stomach is from the pneumogastric and the solar plexus. The former is the chief motor nerve, but section of both pneumogastrics does not completely stop the contractions of the wall of the stomach. The centre which presides over the act of vomiting is situated in the medulla oblongata.

Movements of the Small Intestine.

The movements of the intestine may be observed after opening the abdominal cavity, when, if desirable, they may be intensified by galvanic stimulation, or mechanical irritation. They have also been studied by the aid of some form of *enterograph* (Legros and Onimus, Engelmann, &c.). This instrument consists essentially of an ampulla made of caoutchouc, which is introduced into the intestine, and which communicates, by means of a tube, with a tambour à levier connected with a registering apparatus.

The contractions of the walls of the intestine are always rhythmic, and separated by intervals of repose. They are more active when the intestine is distended with food, and the presence

of bile seems to act as a special stimulant, although this is denied by Schiff. It is also well to remember that they are increased on exposure of the intestine to the air by opening the abdominal cavity.

These movements are of two kinds, *peristaltic* and *anti-peristaltic*, the former favoring progression, the latter having the contrary effect. They are exactly similar to what we have described in the œsophagus during deglutition. The peristalsis is diminished by opium, morphia, and belladonna, while it is increased by the influence of nicotin, muscarin, caffein, and by most purgatives.

Innervation.—The pneumogastric appears to be the motor nerve of the small intestine, and stimulation thereof increases markedly the peristaltic movements, while they are diminished by its section. The splanchnics, on the other hand, appear to have an inhibitory influence.

Movements of the Large Intestine.

Having arrived at the end of the small intestine, the aliments pass without obstruction into the large intestine through the ilio-cœcal opening, while return is effectually prevented by the valve of Bauhin. On account of the peculiar disposition of the large intestine, and the sacculation of its cavity, the transit of its contents is peculiarly slow, and occupies a much longer time than in case of the small intestine, although the course within the latter is so much longer. The movements of the walls are similar to those of the small intestine, and under the same influences. On account of the long detention of the contents of this part of the canal, the aliments, now having assumed the characters of fæces, lose their watery constituents, and tend to assume the solid form. They gradually collect in the sigmoid flexure of the large intestine, where they are generally retained till they descend into the rectum preparatory to defæcation. The peculiar folding of the tube in this situation, and the tonic contraction of O'Beirne's sphincter, are sufficient, when the tone of the muscular wall is normal and the bowels not allowed to become over-distended, to oppose gravitation and the comparatively slow peristalsis of this part of the intestine. On the other hand, when the bowels are neglected and the intestinal wall in an atonic condition,

the descending fæces gradually accumulate in the rectum. Houston believed that the valvular folds of the rectal mucous membrane, to which he called special attention, were of mechanical use in supporting the contents, but this physiological function is very doubtful.

Defæcation.

The pressure of the fæcal matter within the rectum brings on the feeling of desire of defæcation. At first the irritation of the sphincter has the effect of promoting a reflex contraction, by which the escape is more effectually prevented; but if it is allowed to continue, the pressure at last inhibits the tonic contraction of the sphincter, and allows the fæcal contents to escape, even against the will. During normal defæcation, the pressure of the abdominal muscles forces the contents of the colon into the rectum, and the latter part of the bowel is influenced only indirectly by voluntary effort. The contents of the rectum are expelled by the contraction of its own walls, after the sphincter externus has been inhibited by the influence of the will. The longitudinal fibres of the rectum, in contracting, dilate the anal orifice, while the levator ani aids in this action and also presses the posterior surface of the rectum from behind forwards, and raises the inferior extremity above the fæcal mass.

Innervation.—The movements of defæcation are under the influence of a nervous centre, which is placed at the lower part of the lumbo-rachidian bulb (*ano-spinal centre* of Masius). The subject of the *tonicity* of the sphincter shall be referred to in connection with that of the bladder.

Mechanical use of the Intestinal gases.—The presence of the gases of the digestive tube maintains a condition of uniform distension. They also convert the abdominal cavity into a kind of elastic gaseous bag, which distributes the pressure called forth during exertion of any kind, and which, in the act of expiration, presses back the diaphragm by its elasticity.

CHANGES OF THE ALIMENTS IN THE DIGESTIVE TUBE.

In its descent through the alimentary canal, the food undergoes the changes by which it is prepared for absorption. These

digestive changes may be shortly summarised as follows for the different kinds of food :—

A. Hydrocarbons.—*Starch* is converted into dextrin, and then into glucose (or, rather, into achroodextrin, maltose and glucose) by the action of the saliva, pancreatic juice, and, possibly, the bile and intestinal juice. This transformation, which commences in the buccal cavity, progresses, although feebly, in the stomach, but is chiefly effected in the small intestine, where it is completed by the pancreatic juice.

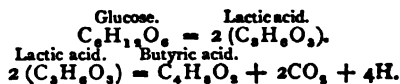
Cane-sugar is dissolved by the saliva and gastric juice, then changed by the action of the inversive ferment of the intestinal juice into inverted sugar (a mixture of equal parts of glucose and lævulose).

Milk-sugar (lactose) is generally believed to be changed into glucose, but its modifications are not well known. It is probably decomposed into galactose and lactoglucose, the reducing power of which is equal to that of ordinary glucose.

Gum and *mucilage* are probably also transformed into glucose.

The digestion of *cellulose* in the alimentary canal of man has been denied by many; but, according to Weiske, who has made numerous experiments on the subject, not more than one-half of the cellulose taken with the food reappears in the excrement, and it is probable that the rest is changed into glucose.

These considerations show that glucose is the essential product of the digestion of hydrocarbons. When the whole of the glucose is not absorbed, it undergoes the butyric fermentation in the digestive tube, and gives birth to lactic and butyric acids.



The same change is undergone by the undigested starch, also sometimes by the cane-sugar, milk-sugar, muscle-sugar, &c.

In certain conditions the glucose undergoes alcoholic fermentation. Cellulose sometimes yields carbonic acid and marsh gas.

B. Fats.—The fats are liquefied in the stomach, and emulsified in the small intestine by the pancreatic juice (slightly, perhaps, by the bile) and by the mixture of soaps and of biliary

acids which are found in the small intestine. At the same time these fats are partly decomposed into fatty acids and glycerine. The acids, when set free, form, with the alkalies of the bile and pancreatic juice, soaps which are soluble and easily absorbed. The subsequent course of the free glycerine is not known; it perhaps undergoes fermentation, giving birth to carbonic acid, hydrogen, fatty acids, succinic acid, &c.

C. *Albuminoids*.—These substances are changed into peptones in the stomach and small intestine by the gastric juice and the pancreatic juice. After the gastric digestion, a part of the peptones formed are precipitated in the duodenum by the bile, and redissolved in the small intestine. To the peptonising stage of digestion another appears to succeed, in which are formed leucin, tyrosin, and some other compounds (xanthin, hypoxanthin, glycocoll, glutamic and asparagic acids, &c.) Following this stage, come putrefactive changes, in which many substances are formed which are found in the fæces (indol, scatol, volatile fatty acid, &c.)

Gelatin is changed by the gastric and pancreatic juices into gelatin peptones, which do not form a jelly on cooling.

D. *Salts*.—The soluble salts are dissolved in the buccal cavity and in the stomach, by the saliva and the gastric juice; the salts of lime and the phosphates of magnesia are partly dissolved in the stomach by the gastric juice, which also decomposes the carbonates, the bases of which combine with hydrochloric or with lactic acid. The salts of organic acids are changed into carbonates.

Absorption by the Digestive Tube.

From the walls of the alimentary canal are absorbed :

(I.) The products of digestion : *alimentary* or *digestive absorption* ;

(II.) A part of the various digestive secretions : *secretory absorption* ;

(III.) Substances which are brought accidentally into contact with the mucous membrane.

I. This absorption deals with the water and soluble salts, albuminoids, glucose, and fats.

A. *Water and soluble salts*.—This takes place chiefly by the laws of osmosis, with the reserve of the special activity of

the intestinal epithelium. Accordingly, if the endosmotic equivalent of the water is very high (as in case of the sulphates of soda and magnesia), this quantity of water is very considerable, and a purgative action results.

B. *Albuminoids*.—These are absorbed in the state of peptones. The absorption begins as soon as the peptones commence to be formed (in the stomach), and it continues actively in the whole length of the small intestine, and in part of the large (cæcum). According to Schiff, gastric absorption takes place only in the pyloric portion, which he calls the absorbing region of the stomach, where the mucous glands are found; in the region of the so-called peptic glands no absorption takes place.

Recent researches (by Brücke, Voit, &c.) tend to prove that this transformation of albuminoids into peptones before absorption is not always essential. According to Eichhorst, gelatin, casein, muscle juice, albuminate of potash, egg-albumin (with the addition of salts), can be absorbed in their unchanged form; while serum-albumin, white of egg, syntonin, coagulated myosin, coagulated fibrin, are the only albuminoids which require to undergo peptonisation. These results have been more recently confirmed by Stockvis, Czerny, and Latschenberg, who have also shown that this absorption of non-peptonised albumin takes place likewise in the large intestine.

C. *Hydrocarbons*.—The glucose, which is the main product of the digestion of hydrocarbons, is very rapidly absorbed in the digestive tube; the absorption commences even in the buccal cavity, when the bolus is kept there for some time. The small intestine is the great seat of the absorption of sugar. In the lower part of the small intestine and in the large, the glucose is decomposed, and gives birth to organic acids (especially lactic), which are rapidly absorbed.

D. *Fats*.—The subject of the absorption of fats is one of the most obscure in physiology. It seems to take place exclusively in the small intestine, and below the entrance of the pancreatic and common cholemic ducts.

The structures chiefly concerned in the absorption are the villi. When examined, from four to eight hours after a meal, they are found to contain enormous numbers of fatty particles, which obscure the whole internal structure. The epithelial cells on the surface are indistinct, and the fatty granules appear to occupy their interior, through which most authorities

believe that the fat passes into the interior of the villus, and so into the central lacteal. The goblet cells, which are found among the cells on the surface, were believed by Letzerich to be special organs for the absorption of fat; but they have been since shown by E. Schultze and Ranvier to be true mucous cells. Kölliker looked upon the striations of the free margin of these cells as formed by a series of canaliculi, through which the lumen of the intestinal canal was placed in connection with the intercellular spaces of the villus, and through which the substances absorbed from the small intestine found their way. Some suppose that these striations are formed by delicate ciliary prolongations, which form a circular rim around the free end of each cell, and leave a central orifice occupied merely by protoplasm. The more probable idea of Klein has been already mentioned in describing the structure of the villi. Klein, however, basing his views on the results of Watney's experiments, advocates a new view of the course of the particles of absorbed fat; affirming that these pass into the interior of the villus, not through the cells themselves, but through the interepithelial substance which cements the cells together. As to the condition in which the fat is absorbed, the following views have been advanced :—

(1) *That it is absorbed in a state of emulsion.*—This is the view advocated by most authorities; that the fat, after division into particles of extreme fineness, passes through the substance of the villus into the central lacteal. The question is not yet, however, satisfactorily settled. The experiments of Funke and Lewantuew have proved that solid fat, however finely divided, will not pass through epithelial cells. On the other hand, fluid fat is not miscible with water, and Vistinghausen has shown that oil will not traverse animal membranes, except when subjected to very high pressure, which does not exist in the intestine. However, it is probable that the presence of the *haptogenous membrane* removes the difficulty, and allows easy adhesion between the fatty particles and the watery contents of the intestine and of the tissues. The presence of the bile must also aid in the absorption, for Vistinghausen has shown that oil traverses animal membranes easily, if previously moistened with bile. If the presence of Kölliker's canaliculi be admitted, capillarity would probably play an important part. According to Thanboffer and Landois, the rods of Brettauer and Steinbach are no other than filiform prolongations of the protoplasm of the cells, and these being possessed of amoeboid movements, grasp the particles of fat, and, surrounding them, draw them into the interior of the cell, in exactly the same way as an amoeba takes in its food, and then pass them on into the interior of the villi. The mobility of these processes they find increased by the presence of the bile, and is, apparently, under the influence of the nervous system. We have already noticed the views of Klein, who affirms that the fatty particles pass into the interior of the villus, through the inter-epithelial cementing substance, and this view would remove some of the difficulties which have been hitherto felt in explaining the phenomena of this variety of absorption.

(2) *That the fat is absorbed in form of soaps.*—The mode of saponification of fats has been already noticed, and it has been generally admitted that soaps are absorbed as such, and pass into the blood. This has been recently denied by Röhrig, who has never been able to find soaps in the

blood; he even asserts that their presence is impossible, for blood plasma in presence of soaps gives a precipitate of the soaps of lime.

(3) *That the decomposed fats are absorbed and reformed by synthesis in the villi.*—This view is supported by the result of the experiments of Perewoznikoff and Will, who found that after injecting into a loop of intestine a mixture of soaps and glycerine, fat appeared in the epithelium and connective tissue of the villi, and passed from this source into the lacteals.

(4) *Theory of Küss.*—According to this view, the formation of fat is due to the nutritive activity of the epithelium, as the particles of fat may be detected in the epithelial cells immediately after being exposed to contact with the chyme, even when the latter contains no fatty matter. The cells swell up, become whitish, and the appearance of the fatty granules in the interior of the villus is immediately noticed.

The absorption of fat is probably limited to the small intestine, but the other products of digestion undergo absorption all along the digestive tube. With regard to the activity of absorption, the various segments of the alimentary canal may be arranged in the following order: small intestine, large intestine, stomach, buccal cavity, pharynx, œsophagus.

The influence of innervation on absorption is obscure, but it has been supposed, as already mentioned, to influence the movements of the amœboid processes of the epithelial cells of the villi, and the contraction of the muscular fibres of the intestinal wall, which may also aid in absorption.

A very hypothetical explanation of the mechanism of the villi in intestinal absorption has been offered by Brücke: the rhythmic contractions of the muscle-cells, which are prolonged over the central lacteal of each villus, shorten the vessel and press out its contents into the subjacent lymphatic; when the contraction ceases, the pressure of the blood in the capillaries causes a kind of turgescence of the villus, with expansion of its lacunæ and of the central lacteal. Regurgitation from the lymphatic beneath is prevented by the valve at the opening, and the result would be to give to each villus the action of a suction-pump.

Secretory Absorption.—The great bulk of the digestive secretions are reabsorbed in their descent along the alimentary canal. Without this reabsorption, the loss to the system would be really enormous. It takes place for the saliva, gastric juice, intestinal juice, pancreatic juice, and a part of the constituents of the bile. A portion of the latter secretion is cast off with the excrements (cholesterin, dyslysin, choloidic acid?); but

about seven-eighths of its solids pass into the blood. Many of these undergo transformation before being reabsorbed; the biliary acids cannot be found in the vena portæ. Schiff, however, believes that bile is absorbed as such, and passing into the blood is again secreted (*biliary circulation*); he has found that injection of bile into the intestine causes increased secretion.

Digestive Absorption.—Alimentary absorption takes place by two kinds of vessels: (*a*) the capillaries, and (*b*) the lymphatics. The first course is that of the great bulk of the water and soluble salts, and probably also of the chief part of the peptones; Cl. Bernard, indeed, believed that the whole of the albuminoids were absorbed in this way. In whatever way they are absorbed, the peptones must be immediately reconverted into albumin, for no substances analogous to peptones can be found in either the blood or chyle. The path of the glucose has been a good deal disputed, but the researches of Cl. Bernard make it very probable that the glucose and inverted sugar are absorbed by the blood-capillaries, and pass up to the liver to be changed into glycogen. The superficial position of the blood-capillaries explains why it is that these substances pass into the capillaries instead of into the central lacteal.

The lacteals are, perhaps, the sole channel of fatty absorption; the facts already mentioned are sufficient proof of this hypothesis. Accordingly, the fats and soaps pass directly to the lung, without first going through the liver.

CHAPTER XII.

RESPIRATION.

THIS act, in its widest sense, consists essentially of a gaseous exchange between the organism and the external medium, air or water, as the case may be. During this exchange, which, in the higher animals, is made between the atmosphere and the circulating blood, the animal absorbs oxygen and eliminates carbonic acid and watery vapour, and the venous blood becomes arterial. The mutual exchange is not confined to a single organ or region exclusively; it goes on over the whole surface of the body, but occurs with special activity in certain parts, which are constructed with a view to the performance of this function.

The Lungs are the organs specialised for the performance of the respiratory function, and may be regarded as an intensely vascular membrane, of very wide extent, but folded in a peculiar way so as to be placed more conveniently within a limited space. Air enters the lungs after passing through the larynx, trachea, and bronchial tubes. The larynx is the upper segment of the windpipe, specially modified for the production of the voice, and requires separate consideration. The *trachea* transmits the air from the larynx to the bronchial tubes, and forming a canal with partially contractile walls, it in some measure regulates the amount of air entering the lungs. The coats of this tube are fibrous (including the cartilaginous rings), muscular, submucous, and mucous. There are eighteen or twenty incomplete cartilaginous rings, connected at the ends by transverse bands of muscular fibres (*trachealis* muscle of Todd and Bowman). The deficiency of the rings is placed behind, so that a transverse section of the tube is D-shaped, and they are imbedded in fibrous tissue, which forms their perichondrium. This investing membrane is very elastic, and allows easy stretching of the trachea to adapt it to the different movements of the neck. The submucous tissue is moderate

in quantity, and contains numerous mucous glands, the secretion of which lubricates the interior of the tube. The basement membrane supports a lining of ciliated columnar epithelial cells, the waving of whose processes towards the laryngeal end of the tube, aids in the removal of mucus and particles of foreign matter. The structure of the bronchial tubes is similar to that of the trachea. The right is the larger and shorter. On division, the branches have, at first, complete rings, between which the muscular tissue forms circular bundles (*muscles of Reisseissen*), going all round the tube. The tubes divide dichotomously as they



Fig. 57.
Epithelium from trachea of cat.

pass into the lung substance, and when they reach a diameter of about $\frac{1}{16}$ of an inch they terminate in expanded extremities called *infundibula*. These are lined by flattened cells, which present the appearance of endothelium. They are known to be epithelial by their hypoblastic origin, and by the fact that before respiration the alveoli of the foetal lung are lined by columnar cells, which are afterwards flattened out by the pressure of the inspired air. This lining membrane is thrown into elevations, which enclose honey-comb depressions (*alveoli* or *air-cells*). In the thin parti-



Fig. 58.
Lobule of lung.

tions the capillaries are found ramifying, an arrangement which has the effect of exposing the blood to the air on two surfaces. At the neck of the infundibulum, the muscular fibres form a strong annular band (*sphinder of Rindfleisch*), where they terminate. Elastic membrane forms the wall of the infundibulum.

The whole of the aërial tree is represented by a cone, of which the truncated summit is formed by the trachea, while the base is at the pulmonary alveoli. The exchange of gases, which is the

essential phenomenon of respiration, takes place between the blood on one side of this membrane and the atmospheric air on the other. In order to keep up the necessary uniformity of the exchange, there must be a continuous circulation of blood on one side and of air on the other. The former is regulated by the various dispositions which have been already considered; the latter kept up by the respiratory movements, to which we have next to direct our attention. As the lungs are never completely emptied, the air which is taken into the chest during each respiratory movement never penetrates at once to the alveoli, so that the exchange of gases between the pure and the impure air takes place simply by diffusion; and this process of *pulmonary ventilation* consists of two parts, inspiration and expiration. The former is the action by which air is drawn into the lungs; the latter corresponds to the imperfect emptying.

The *thorax*, looked at from a physiologist's stand-point, forms an elastic case, of which the mobile walls can increase the size during inspiration, and diminish it during expiration. The different regions of the thoracic walls take very different parts in the expansion of the cavity, according to their structure. The natural position (position of equilibrium) corresponds to the state of ordinary expiration. The chest-wall is drawn from this condition of rest by the action of numerous muscles. Some of these have the effect of increasing the thoracic cavity (*muscles of inspiration*), while others diminish it (*muscles of expiration*). Inspiration and forced (*extraordinary*) expiration are the result of muscular action; while the act of ordinary expiration (or return of the chest-walls to equilibrium) takes place simply by the elastic recoil of the lung tissue and chest wall, which follows the lung to its former position of equilibrium.

The thoracic cavity is hermetically closed; so that the atmospheric air cannot act on the *external* surface of the hollow organs which it contains (lungs and heart), while it acts on their internal surfaces either directly, as in case of the lungs, or indirectly (by means of the blood), as in case of the heart and great vessels.

The elasticity of the lung plays an essential part in respiration. During the inspiratory expansion of the thoracic cavity, the elastic walls of the alveoli yield to the atmospheric pressure,

in consequence of which the expanding lung follows the movement of the chest-wall. When the contraction of the inspiratory muscles ceases, this elasticity of the pulmonary alveoli enters into play and forces out the air, while the chest-wall follows the contracting lung. But in the normal state of things the atmospheric pressure, exerted through the air passages, prevents the lungs from ever attaining the full limit of their elasticity. Accordingly, when an opening is made in the chest-wall, by which air is admitted into the pleural cavity, and the pressure on both surfaces of the lung is equalised, the pulmonary elasticity enters into full play, and the lung retracts, expelling the air which it contains. This elasticity has been shown by Carson to be able to support 6—8mm. of mercury (by the experiment of adapting a mercurial manometer to the trachea of an animal, and then incising the thoracic wall).

The pulmonary *contractility* is less easy to determine, and has been greatly disputed. The results of Williams were controverted by Wintrich, Rugenberg, and other physiologists, but have been more recently confirmed by the elaborate experiments of Bert. The first-named observer found that galvanisation of the lung caused retraction and expulsion of air, so as to blow out a candle, or cause the ascent of water in a manometer connected with the trachea. Bert has applied the graphic method to this experiment, and obtained well-defined results.

Inspiration.—This is essentially a muscular act. The muscles which produce it have the following obstacles to overcome : (1) the elasticity of the thoracic wall ; (2) the elasticity of the lung ; (3) the negative pressure of the intra-pulmonary air in inspiration. The value of the first factor has not been calculated ; that of the second has been estimated at 8mm. of mercury in calm inspiration, while it reaches a mean of 24mm. during deep inspirations ; the third varies from 1mm. in calm inspiration, to 57mm. when a deep breath is taken. By this calculation the inspiratory muscles have to surmount (neglecting the thoracic elasticity) a resistance of $8 + 1 = 9$ mm. during quiet inspiration, and of $24 + 57 = 81$ mm. during a labored inspiration.

Ordinary expiration is produced solely by the elastic recoil of the lung tissue and chest-wall, without the intervention of any muscular force. In forced *expiration*, the abdominal muscles intervene ; they have to overcome a resistance equal

to the pressure of the intra-pulmonary air in expiration, less by the pulmonary elasticity ($87 - 24 = 63$ mm. of mercury), and a still greater pressure in severe efforts.

The muscles concerned in the inspiratory act are usually divided into *ordinary* and *extraordinary*. The former alone are called into play in quiet respiration. They are the diaphragm, scaleni, levatores costarum, and intercostals. The action of the intercostal muscles has given rise to a great deal of discussion, but the more favored idea now is, that the external, with the parts of the internal placed between the costal cartilages, are inspiratory, while the remaining portions of the internal intercostals act as muscles of expiration.

The descent of the diaphragm, caused by its contraction, and the diminution of its upward convexity, has the effect of increasing the vertical measurement of the thorax. At the same time the contraction of the scalene muscles fixes the two first ribs, which give a point of support for the contraction of the external intercostal muscles. The latter, aided in the dorsal region by the levatores costarum, raise the ribs, at the same time causing them to rotate around the axis connecting their vertebral and sternal attachments. This complex movement has the effect of increasing the transverse horizontal diameter of the chest, while the simultaneous forward movement of the sternum, especially at its lower part, caused by the resistance of the ribs and costal cartilages, causes an increase in the antero-posterior measurements.

Among the muscles called into play during labored inspiration, the more important are the sterno-cleido-mastoid, serratus posticus superior, levator anguli scapulæ, trapezius (upper part), pectoralis minor, pectoralis major (lower part), serratus anticus magnus, and cervicalis descendens. According to Cleland, the serratus posticus inferior, by tending to expand the base of the thorax, also acts as an inspiratory muscle.

The muscles of expiration are all extraordinary, as, in quiet breathing, muscular effort is not called for during this part of the act. The principal are: internal intercostals, infracostales, triangularis sterni, abdominal muscles, serratus posticus inferior (?), sacro-lumbalis, latissimus dorsi, quadratus lumborum, levator ani.

The expansion of the thorax varies over different parts of its surface. The epigastrium presents the widest range of excu-

nion ; the most limited movement is, according to Ackermann, in the fourth intercostal space.

The dilatation of the lung also varies according to the different points of its surface ; the most fixed parts are the roots, and the most moveable are those farthest from these fixed points, especially the anterior and inferior borders.

To allow the passage of air into the lungs, it is necessary that the air-passages should be fully open. At each inspiration, the nostrils are dilated by the levator *alæ nasi*, and the dilatores *alæ nasi* ; this nasal movement is seen in man only in labored inspirations, and especially in children. It is extremely well marked in some animals, especially the horse. Passing into the nasal fossæ, the air is warmed and charged with watery vapor. These changes are provided for by the rich vascularity of the mucous membrane, and the large superficies afforded by the extreme irregularity of the surface. When the air passes into the mouth it does not receive the same amount of warmth and moisture, and on this account is not so healthy for the lungs.

At the moment of inspiration the *larynx* is lowered, whilst the *trachea* is dilated. The reverse conditions are seen in expiration.

The *glottis*, during moderate inspiration, presents the form of a triangular opening, of which the base is placed behind, and somewhat enlarged in the inter-arytænoid portion ; during a forced inspiration it is very much widened. During expiration the vocal chords approach one another, and form an isosceles triangle.

The *abdominal pressure* increases during inspiration, from the compression of its contents by the descending diaphragm ; it diminishes during an ordinary expiration.

Respiratory murmur.—On application of the ear to the surface of the chest, either directly or with the intervention of a stethoscope, a soft, breezy sound is heard during inspiration. The name of *vesicular murmur* has been given to this sound as it is generally believed to be produced by the sudden distension of the pulmonary vesicles with air, and the friction of the gaseous molecules against their walls. A similar bruit, but more feeble, and lasting for only a third of the time, is heard at the beginning of the expiratory movement. At the level of the larynx, trachea, and larger tubes (in the inter-scapular region, at the

level of the fourth dorsal vertebra), a blowing sound is heard, the *bronchial soufflet*, which is louder than the other, and is heard equally well during expiration.

Rhythm and number of the respiratory movements.—A single respiration is made up of two stages, (a) *inspiration*, and (b) *expiration*. Most authorities admit the existence of an *expiratory pause*, following the movement of expiration, during which there is a complete repose of both inspiratory and expiratory forces. The respiratory graphic tracings (obtained by introducing into the trachea of an animal the tube of a registering tambour) show that in ordinary, quiet respiration, there is a slight pause between the inspiratory descent and the expiratory ascent, while in rapid respiration this pause completely disappears. In most cases, the comparative slowness of the expiratory act towards its termination allows the latter part of the expiratory curve to assume almost the course of a horizontal line.

Some observers have also admitted the existence of an *inspiratory pause*, occurring at the end of inspiration; but it does not exist in the normal condition.

In ordinary respiration, then, it may be said that there are but two stages: inspiration and expiration. The expiratory act is a little the longer of the two, but the exact proportion is hard to calculate; it is generally estimated at 10 : 12.

The inspiratory movement is at first very rapid, but soon becomes slower; and at its termination, without any interval, it passes into the expiratory movement. The total duration of a respiratory movement varies greatly, and the mean duration has been very variously estimated (12—24 per minute). In a state of perfect rest, the number of respirations per minute is not more than twelve. It is generally calculated at seventeen or eighteen per minute. They are, usually, perfectly regular, but can be quickened or slowed by voluntary effort, or even stopped altogether for a limited time. The respiratory movements are quickened by muscular exertion (walking, running, &c.), and also by mental activity. Certain mental emotions, however, may arrest them entirely for a short time. Attention directed to the act has the effect of disturbing the respiratory rhythm.

The influence of the *nervous system* on respiration has been already studied with the physiology of the medulla oblongata.

Age influences the frequency of the respiratory movements: it is greatest in infancy, and diminishes with advancing age. *Compression* of the chest, or of the respiratory passages, diminishes the frequency of the respiratory movements, while it increases their amplitude in the former case, but diminishes it in the latter. *Elevation of temperature* increases the frequency. They are also influenced by *stature*; as a general rule the frequency is in inverse ratio to the height of the individual (man or other animal).

Cheyne-Stokes respiration.—This is a peculiar modification of the respiratory movement which is seen in certain pathological conditions (fatty heart, of which it was originally believed to be a pathognomonic symptom; atheroma of the aorta; certain cerebral affections, &c.) It consists of respiratory pauses alternating with a series of respirations which, at first very superficial, gradually increase in amplitude till a maximum depth and rapidity is reached, after which they gradually diminish till they end in another pause.

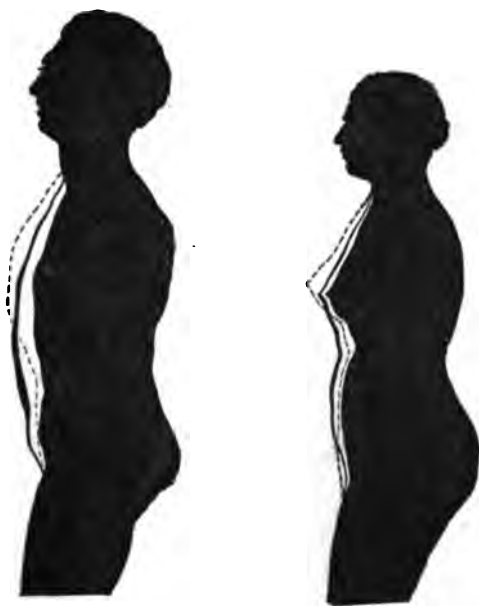


Fig. 59.
TYPES OF RESPIRATORY MOVEMENTS (Male and Female.)

Types of respiration.—Among all the inspiratory muscles the different groups do not present the same degree of activity, and according as the action of one group or another predominates, we have different forms of enlargement of the thoracic cavity. When the action of the diaphragm predominates, the respiration is called *diaphragmatic* or *abdominal*; the abdomen swells out, and the horizontal measurements of the thorax are but slightly modified, except in the inferior parts. This mode of respiratory movement prevails in man. In the *costal* (*thoracic*) type, on the other hand, the enlargement of the chest is chiefly in its transverse diameters, and the action of the diaphragm is but little marked. The abdomen remains flattened, and the movements are almost confined to the ribs. This form of respiration is met with in women, in whom it would seem to be due to the effects of tight lacing. It is sometimes divided into two kinds, *superior costal* and *inferior costal*, according as the expansion of the upper or lower part of the chest is the more pronounced. When the former is specially marked the movements of the clavicle and the two first ribs become very marked, and the resulting type receives the name of *clavicular respiration*.

Fig. 59 represents the types of the respiratory movement in man and in woman. During sleep there is diminished action of the diaphragm, and the respiration assumes the clavicular type (Mosso).

Special respiratory acts. Inspiratory.—These acts are sometimes simple, as in suckling or snuffing, sometimes more complex, as in yawning. In the act of *suckling* the air passes through the mouth, drawing in the liquid in contact with the buccal orifice. In *snuffing* the current of air passes through the nose, and draws with it the foreign body placed in contact with the nostril. *Yawning* is a deep inspiration, with the mouth widely opened, accompanied by contraction of certain muscles of the face, and followed by an expiratory movement, sometimes noisy, sometimes silent. *Sobbing* consists of a series of diaphragmatic inspirations, short, spasmodic, and painful, with lengthening of the glottic sound both in inspiration and expiration. In *sighing* the inspiratory movement is slow and deep, followed by short but forcible expiration, accompanied by a characteristic sound. *Hiccup* is a spasmodic contraction of the diaphragm, with sudden inspiration, stopped abruptly by approximation of the vocal chords.

Expiratory.—*Coughing* consists of one or more sudden expirations, with narrowing of the rima glottidis, and production of sound of variable loudness; the current of expired air passes chiefly by the mouth. *Expectoration* is the expulsion by cough of the mucus contained in the larynx

and trachea. In *clearing the throat* (*hem-ing*, *excretion* of the French writers), the mucus collected in the back of the mouth and pharynx is carried outwards with the current of expired air. In *spitting*, the current of expired air carries out the mucus of the buccal cavity; in *blowing the nose*, the current of air, instead of passing through the mouth, passes through the nasal fossæ. *Sneezing* consists of a deep inspiration, followed by a sudden expiration, in which the current of air is directed through the nasal fossæ. *Laughing* is made up of a series of successive expirations, with the mouth open, and with the production of a special sound at the rima glottidis; during this act, the epiglottis is raised, and the passage of foreign matters into the larynx is facilitated.

Apnoea.—When the blood is saturated with oxygen the respiratory movements cease, as was long ago observed by Hook (1667); it is to this state that Rosenthal (1854) has given the name of *apnoea*. If insufflation of the lungs be practised on an animal, while the intervals between the successive insufflations is gradually diminished, the respiratory movements become gradually slower, and at last completely cease; but the other vital functions proceed at the normal rate.

Dyspnœa.—The phenomena of dyspnœa are always present when the gaseous changes are not taking place in the lungs with sufficient activity. They may be produced in one of two ways: (*a*) by opening the pleura, which leads to collapse of one or both lungs; (*b*) by narrowing of the respiratory passages, which at once diminishes the amount of air entering the lungs. Whatever be its mode of production, dyspnœa is manifested by exaggerated movements of inspiration; both ordinary and extraordinary muscles of inspiration are thrown into play, and the larynx, which is nearly immobile in ordinary respiration, is greatly depressed, which is one of the characteristic signs of dyspnœa.

Asphyxia.—In considering the phenomena of asphyxia, it is necessary to distinguish between the *rapid* asphyxia produced by complete obstruction to the entrance of air, such as in occlusion of the trachea, and *slow* asphyxia, in which the obstruction is gradually established.

The phenomena of asphyxia are divisible into three stages, which are easily observed in animals, especially the dog. In the first stage, which lasts about a minute, the phenomena of dyspnœa appear in the beginning, the forced inspiratory movements are very marked, especially for the thoracic muscles; the abdominal muscles then contract forcibly, and at the end

of the first minute *convulsions* appear, which are at first purely *expiratory*, and afterwards accompanied by spasms, more or less irregular, of the limbs, especially of the flexor muscles.

In the *second stage*, which lasts about the same time, the convulsive actions cease, sometimes quite *suddenly*; the expiratory movements at the same time are scarcely perceptible; the pupil is dilated; the eyelids do not close when the cornea is touched; reflex actions have ceased; all the muscles, except the inspiratory, are in a state of relaxation; the arterial pressure is lowered; there is, in short, a state of general calm, which contrasts forcibly with the agitation of the first stage.

In the *third stage*, which last from two to three minutes, the inspiratory movements become more and more feeble and widely separated; the extraordinary muscles of inspiration contract spasmodically, and soon after, the spasms pass to other muscles, especially the extensors; the head is thrown backwards, and the extension proceeds to complete opisthotonos; the limbs are stretched; the nostrils dilated; convulsive yawning movements take place, and in one of these, death steps in and closes the scene.

The phenomena of *slow* asphyxia follow a similar course, although with less rapidity; but the successive stages of *expiratory convulsions*, *calm*, and *inspiratory convulsions* are found, as in the other case.

Air in Respiration.

Inspired Air.—About 500 cubic centimetres of air are taken into the chest at each inspiration, or 9,000.cc. in twenty-four hours. As air is the agent by which all the respiratory changes are effected, it is necessary for us to understand its nature and composition. Atmospheric air contains, in 100 parts:—

Oxygen,	..	In volume, 20.9.	In weight, 23.
Nitrogen,	..	„ 79.1.	„ 77.

Proportionally minute traces of carbonic acid and of watery vapor are also present. The proportion of CO₂ varies from 2 to 4 parts in 10,000. It is greater in densely habited

districts than under opposite circumstances, and greater during the night than in the day.

The quantity of *watery vapour* varies with the temperature of the air; it is greater as the latter is more elevated, and accordingly is greater in summer than in winter. The *humidity* (*hygrometric state*) of the atmosphere, however, does not depend on the absolute proportion of watery vapor present, but whether it is more or less near the point of saturation. Accordingly, the air is drier in summer than in winter, although it contains more watery vapor. The *hygrometric state* is expressed by the *fraction of saturation*; that is to say, the quantity of watery vapor contained in the air divided by the quantity which the air requires for saturation at the same temperature.

(a) *Tidal air*.—The amount of the *tidal* or *breathing* air is about 500 cc. (30—35 cubic inches).

(b) *Complemental air*.—This is the quantity of air which we are able to inspire with the greatest effort, over and above the tidal air. It is estimated at about 1,670 cc.

(c) *Reserved air*.—This is the quantity of air remaining in the lungs after an ordinary expiration, which can be expelled by the fullest effort. The average amount is about 1,600 cc.

(d) *Residual air*.—The amount which remains in the lungs after the fullest possible expiration, and cannot be expelled by any voluntary effort. It represents a mean quantity of 1,200 cc.

Vital capacity.—The quantity $a + b + c$ represents the *vital capacity* of Hutchinson. It is found by making the most powerful expiratory effort after the fullest possible inspiration. The term “extreme differential capacity” is preferred by some writers.

Pulmonary capacity.—The quantity $c + d$ represents the *pulmonary capacity* of Grehant.

The following numbers are from Hutchinson :—

<i>Residual,</i>	..	Volume,	from	40	to	260	cubic inches.
<i>Reserve,</i>	..	..	..	77	..	170	
<i>Breathing,</i>	..	..	..	3	..	100	
<i>Complemental,</i>	..	..	..	119	..	200	
<i>Vital capacity,</i>	..	..	..	100	..	300	

The next table is also taken from the same observer, and gives the vital capacity at three periods of life, from 4,800 cases (males):—

Height.		Age.		
		15—35	35—65	65—75
5 ft. 0 in.	to 5 ft. 1 in.	174	163	161
5 1	„ 5 2	182	173	168
5 2	„ 5 3	190	181	175
5 3	„ 5 4	198	188	182
5 4	„ 5 5	206	196	190
5 5	„ 5 6	214	203	197
5 6	„ 5 7	222	211	204
5 7	„ 5 8	230	219	212
5 8	„ 5 9	238	226	219
5 9	„ 5 10	246	234	226
5 10	„ 5 11	254	242	234
5 11	„ 6 0	262	249	241

Besides the marked influence of stature and of age, the vital capacity is affected by weight. Above $11\frac{1}{2}$ stones it falls 1 cubic inch for each pound added.

For the purpose of measuring the vital capacity, Hutchinson invented the *spirometer*, in which a hollow cylinder is inverted within another cylinder containing water. Air blown in through a tube rose in the water, and elevated the inner one; the degree of elevation depending directly on the amount of air, which is read off on a graduated scale.

Besides these constant constituents, the air may contain a variable quantity of mineral powders, products of decomposition, organic substances, carbonate of ammonia, carbonated hydrogen, phosphuretted hydrogen, sulphuretted hydrogen, nitric acid, nitrate of ammonia (Schönbein), ozone, antozone, volatile principles of organic origin, organic germs, &c.

Two conditions of the air influence respiration: (a) temperature, and (b) pressure.

(a) The temperature of the atmospheric air varies very widely. When air is expanded by heat, it becomes rarified, and the actual quantity of oxygen which a given bulk contains is diminished. Each inspiration causes about a demi-litre of air to enter the lungs, which contains about .104 litre of oxygen at a temperature of 0° C. (32° F.). At 40° C. (104° F.) this demi-

litre of air contains but .0915 litre of O. The coefficient of dilatation of air is .00367, so that 100 vols. of air at 0°C . (32°F .) become 114 volumes at 40°C . (104°F .). On this account we are obliged, when the temperature undergoes any

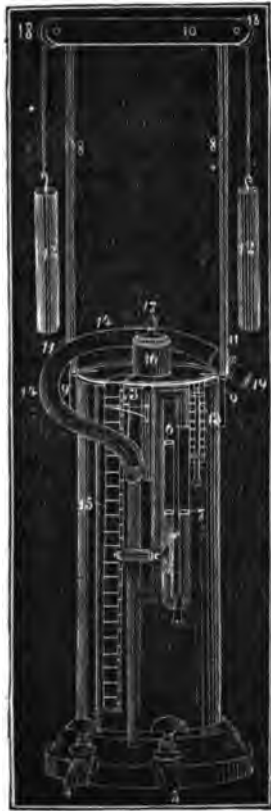


Fig. 60.—Hutchinson's Spirometer.

considerable elevation, to increase the number and depth of our respirations, in order to introduce the necessary amount of oxygen.

The *pressure* of the atmospheric air has a mean of 760 mm. at the level of the sea, but the point of greatest importance to note, in connection with the exchange of gases, is not the total barometric pressure, but the *partial pressure* of each of the gases of the atmosphere, and especially of oxygen. These partial pressures are proportional to the quantities of gas contained in the atmospheric air.

$$\begin{aligned}\text{Pressure of O} &= \frac{760 \times 20.8}{100} = .158 \text{ mm.} \\ \text{,, N} &= \frac{760 \times 79.2}{100} = .601 \text{ mm.} \\ \text{,, CO}_2 &= \frac{760 + .00025}{100} = .002 \text{ mm.}\end{aligned}$$

The pressures are somewhat different in the interior of the lung.

(2) *Expired air*.—The composition of the expired air is as follows compared with the inspired air :—

		Expired air.		Inspired air.
Oxygen,	..	15.4	..	20.9
Nitrogen,	..	79.3	..	79.1
Carbonic acid,	..	4.3	..	..
		99.		100.

The following characters distinguish it from the inspired air :—

- (1) It contains less oxygen ;
- (2) It contains more carbonic acid, the presence of which is easily demonstrated by breathing into lime water ;
- (3) It contains a little more nitrogen ;
- (4) It is saturated with watery vapor, which comes from the mucous membrane of the respiratory tract ;
- (5) The temperature approaches that of the body ; the temperature of the inspired air is variable.
- (6) The bulk of the expired air, if taken at the same temperature as the inspired, is found to be slightly diminished (99 : 100). This is due to the fact that more oxygen (5.5 per cent.) disappears than returns in the form of carbonic acid (4.3 per cent.).

Expired air also contains traces of ammonia (Davy) ; this has been supposed to come from the decomposition of nitrogenous substances in the buccal cavity, but was found by Losson in the air of the trachea. The daily amount exhaled would be

about .0104 gramme. Traces of carburetted hydrogen and of sulphuretted hydrogen have also been demonstrated; these come from the intestinal gases which pass into the blood. Other volatile substances of deleterious nature are also present, but have not been isolated. The presence of numerous other excretory products (chloride of sodium, chloride of ammonium, uric acid, urates of soda and ammonia) has been reported by Wiederhold; but their existence is doubted by most physiologists.

The volume of expired air is nearly equal to that of the inspired. It is usually larger, on account of the expansion caused by the elevation of temperature, and addition of watery vapor. But if reduced to the same temperature and dried, the quantity is found to be a little less than the inspired (99 : 100). The change is due to the fact, long ago noticed by Lavoisier, that in inspiration more oxygen is used up than returns in the form of carbonic acid. In the change which take place within the lungs ($20.9 - 15.4 =$) 5.5 parts of oxygen are lost which are replaced by 4.3 parts of carbonic acid.

Movement increases the amount of the tidal air. Taking the volume of air expired in the dorsal decubitus at unity, the following table shows the proportion of air expired under different conditions (Smith) :—

Dorsal decubitus	.	.	.	1
Sitting position	.	.	.	1.18
Reading	.	.	.	1.26
Standing upright	.	.	.	1.33
Walking (slowly)	.	.	.	1.9
" (rapidly)	.	.	.	4.0
Running	.	.	.	7.0

Composition of the air in the lungs.—The intra-pulmonary air has not a constant or uniform composition; it is not the same in the different parts of the air-passages, and is modified by the frequency and depth of the respiratory movements. The air contained in the deeper parts is poorer in oxygen, but contains more carbonic acid and watery vapour. If the expired air be divided into two equal parts, the first portion which comes from the upper segment of the aerial tree contains less carbonic acid (3.7 per 100) than the second portion (5.4 per 100) which comes from the deeper parts (Vierordt). This difference of composition is in itself sufficient to establish *currents*

of diffusion ; a current of oxygen passing from above downwards and a current of carbonic acid passing from below upwards. If the respiratory movements be entirely stopped, and the open mouth be placed in communication with a reservoir of air, appreciable quantities of carbonic acid soon find their way into the latter. These currents are sufficient to keep up the respiratory changes during hibernation and other conditions, when the respiratory movements seem to have entirely ceased.

The residual air must contain a larger proportion of carbonic acid than the expired air. It is difficult to calculate it with any degree of precision. By paying special attention to the latter parts of the reserved air, it has been estimated at about 7—8 per 100. Its composition is, of course, continually changing ; with each inspiratory movement purer air passes into the alveoli from the tubes above.

Change of air in the vesicles.—The pure air does not find its way to the air-vesicles directly ; it merely passes into the larger tubes, where currents of diffusion are immediately established between it and the impure air lower down. About 500 cc. of air are admitted into the lungs at each inspiration. A quantity (practically) identical with this is expelled with the next expiration. Of this we are justified in saying that 170 cc. of pure air are expelled with the impure air already contained in the lungs. This is shown by Grehan's experiment of substituting hydrogen for the pure air, when 170 cc. of hydrogen are found expelled with 330 cc. of pulmonary air. Accordingly we may say that in each respiratory movement two-thirds of the tidal air remain in the lungs, while one-third is expelled with the impure air. The pure air which remains in the lungs is, accordingly, uniformly distributed in about five respirations.

The quotient obtained by dividing the quantity of inspired air by the pulmonary capacity, has been called by Grehan the *co-efficient of ventilation*. It increases in proportion to the volume of air, but only within certain limits.

Pressure of air in the lungs.

During inspiration the pressure of the air in the respiratory tubes is *negative* (less than the atmospheric pressure). The negativity varies from — 1 mm. of mercury, during calm inspiration, to — 57 mm. in labored inspiration.

During expiration the pressure in the bronchial tubes becomes positive, and varies from 2 or 3 mm., during quiet expiration, to 87 mm. during labored expiration.

Function of blood in respiration.

The respiratory movements and changes are modified largely by the quantity and quality of the blood, the rate of its circulation, the proportion of gases which it contains, &c.

Composition of the blood.—Certain constituents of the blood have a definite chemical affinity for the respiratory gases; these are the hæmoglobin and certain salts of the plasma. The hæmoglobin fixes the oxygen in definite proportion, forming oxyhæmoglobin. The properties and functions of this substance have been described with the circulation. Some of the plasma salts seem to fix the carbonic acid in a state of loose chemical combination; these are the carbonate of soda, and probably the phosphate of soda (Fernet). The red corpuscles have also the power of fixing a certain quantity of carbonic acid in a combination still unknown (A. Schmidt, Mathieu, Zuntz, &c.)

Proportion of the gases of the blood.—The average proportion of gases obtained from the two kinds of blood is as follows (measured at 760 mm. and 0°C.) :—

From 100 vols.	Oxygen.	Carbonic acid.	Nitrogen.
Arterial, ...	20 vols.	39 vols.	1·2 vols.
Venous, ...	8-12 „	46 „	1·2 „

Pressure of the gases of the blood.—This has been estimated in the following way by Wolffberg. By the aid of a special instrument, the *pulmonary catheter*, the air of a given lobule or lobules of the lung, in which the blood still circulates, may be isolated, while respiration still continues in the other parts of the lung; at the end of a certain time when the pressure is equalized between the carbonic acid of the blood and that of the isolated lobule, the gases of the latter are analysed.

Also, if the blood taken from any of the vessels of the body be agitated with oxygen or carbonic acid, the tension of the gases after the agitation has ceased is equal to that of the gases of the blood. We have then the following data: the quantity and tension of the gas first taken, the quantity lost by the blood, and the tension of the mixture. From these data the calculation is easily made. To measure the tension a special apparatus

has been made by Pflüger and Strassburg, to which they have given the name of *aeortonometer*.

These methods have given the following results (Strassburg) :—

	Tension of O.	Tension of CO ₂ .	Proportion of O.	Proportion of CO ₂ .
Arterial Blood	29.60	21	3.9	2.8
Venous Blood	22.	41	2.9	5.4

For man these figures are probably too low, the proportion of CO₂ in the air vesicles, as we have already seen, probably amounts to 7 or 8 per cent.

The fact that the greater part of the gases present in blood are combined (the oxygen with the hæmoglobin, and the carbonic acid with the plasma salts) tends to complicate greatly the calculation of the influence of pressure on their absorption and elimination.

Respiratory surface.

The respiratory surface is formed by the pulmonary vesicles, of which the number has been calculated approximately at 1,700 to 1,800 millions representing a total surface of about 200 square metres. The pulmonary capillaries cover about three-fourths of this surface, or an area of 150 sq. m. (Küss).

The pulmonary tissue is itself an important agent in the exchange of the respiratory gases as we shall see further on.

Exchange of gases.

The exchange of gases that takes place between the blood and the intra-pulmonary air follow, in a great measure, the physical laws of the absorption and diffusion of gases. Many explanations were formerly offered of the nature of the process. It was at one time supposed that the carbonic acid was directly formed, by combination of the inspired oxygen with the carbon of the effete matter conveyed to the lungs. It was suggested by Liebig that the carbonic acid of the venous blood was combined with the iron in the form of a carbonate of protoxide, and that in the lungs the oxygen displaced the carbonic acid and joined with the iron to form a peroxide.

But we do not now believe with Magnus that there is a direct displacement of carbonic acid by oxygen. When a gas,

such as oxygen, is placed in presence of a liquid, the absorption of that gas depends, *æsteris paribus*, on the excess of the pressure of the external oxygen over that contained in the liquid, while the pressure of another gas, such as hydrogen, has no influence. The same rule holds good for any gas absorbed.

But the gases of the blood are not in a state of simple solution, and they are, in consequence, subject to laws widely diverging from that given above, which is generally known as the *Henry-Dalton law*, or law of pressures.

The exchange of gases consists of four different acts: absorption of oxygen, elimination of carbonic acid, nitrogen, and watery vapor. For the better understanding of these processes we must consider, for a little, the principal laws which govern gaseous exchanges.

Absorption of gas.—The absorption of gases by liquids follows this law. For the same gas, and the same liquid, at the same temperature, the volume of the gas absorbed or dissolved by the liquid is constant, whatever be the pressure to which it is subjected. Carbonic acid, ammonia, &c., are very easily absorbed; oxygen, hydrogen, and nitrogen, with much greater difficulty. The amount of absorption is measured by certain instruments called *absorptimeters* (Henry's, Bunsen's, &c.). As the density of a gas is proportional to the pressure to which it is subjected (Mariotte's law), it follows that the weight of a gas absorbed by a given weight of liquid is proportional to the pressure under which the absorption takes place. The *coefficient of absorption* of a gas for a liquid is the volume of that gas dissolved by a unit of the liquid; it diminishes as the temperature of the latter is raised, and at the boiling point is = 0.

The absorption of gases by solids consists simply of a condensation of the gas on the surface of the substance. The amount absorbed depends on the nature of the body and that of the gas; the order in which they are ranged.

Diffusion of gases.—When two gases are brought together in a closed space, a double current is at once established till the two gases are intimately mingled, and the homogeneity of the mixture is completely established. The diffusion is completely independent of their density, and their presence does not cause any mutual pressure.

Osmosis of gases.—When a lamina of porous material is placed between two gases diffusion takes place as in the preceding case, but with variations depending on the pressure and density of the gases, and also on the nature of the diaphragm interposed. According to Graham, the rate of osmosis is in inverse ratio to the square roots of the densities of the gases. When the membranes used are moist, absorption of gas by the moistening fluid must precede the osmotic diffusion. The osmosis of gases has been studied by Faust, Beclard, and more particularly by Boulland, by the aid of an instrument to which he has given the name of *osmopneumeter*, constructed with the fibrous coat of a frog's stomach. Among other important results obtained, he found that nitrogen drew towards it all the other gases tried but

did not endosmose to any; its greatest attraction was for carbonic acid. Oxygen (and, accordingly, air) drew towards it most other gases especially carbonic acid.

Absorption of oxygen.—With each inspiration of 500 cc., of air 100 cc., of oxygen is inhaled, of which but a third is expelled with the succeeding inspiration, leaving two-thirds to be absorbed by the blood of the pulmonary capillaries. Calculated in this way, about 516,500 cc (744 grammes) of oxygen, are absorbed during 24 hours (at 0°C and a pressure of 760 mm.).

Two conditions influence the absorption of oxygen: *chemical affinity* and *pressure*. By the former agency the oxygen is taken up by the red corpuscles of the blood, after passing into the plasma. Some physiologists believe that the total quantity of oxygen is dissolved in the plasma before passing to the hæmoglobin. There can be little doubt, then, that pressure plays a very important part in the absorption of this gas, and the following table, which gives the various pressures of the oxygen in the pulmonary vesicles, and in the blood during the different parts of the respiratory act, shows the pressure under which the absorption is carried on.

Pressure of oxygen.

	In pulmonary capillaries.	In the air vesicles.	Difference.
Quiet inspiration	44mm.	129mm.	85mm.
Deep inspiration	44 "	140 "	96 "
Quiet expiration	44 "	121 "	77 "
Deep expiration	44 "	110 "	66 "

This table shows that absorption of oxygen takes place during expiration as well as inspiration, although to a less extent. The affinity of the red corpuscles for oxygen explains the fact that when an animal is made to respire in a closed space, the oxygen gradually diminishes, and ends by disappearing altogether, even although the space had been originally filled with the pure gas.

The amount of oxygen absorbed is increased by exercise, by cold, &c.

Elimination of carbonic acid.—500 cc. of expired air contain about 21.5 cc. of CO_2 , which represents a daily elimination of 455,500 cc. (900 grammes) of this gas. The elimination of the carbonic acid of the blood from the pulmonary surface, seems to follow, in greater part, at least, the physical laws of diffusion

of gases ; and the difference of pressure of the gas of the blood, and that of the air of the pulmonary vesicles, plays the most important part in the exchange.

Tension of carbonic acid.

	In the blood of the pulmonary capillaries.		In the air of the alveoli.		Difference.
Calm inspiration	. 82 mm.	..	30 mm.	..	52 mm.
Deep "	. 82 "	..	7 "	..	75 "
Calm expiration	. 82 "	..	38 "	..	44 "
Deep "	. 82 "	..	67 "	..	15 "

The elimination of carbonic acid takes place chiefly at the time of inspiration. Where the respiratory movements are deep, the impure air is rapidly displaced from the alveoli, and replaced by the purer air from above. When the respiratory movements are stopped, the carbonic acid accumulates in the pulmonary vesicles, and a point may be reached at which the pressure of the gas in the air-vesicles comes to equal that in the pulmonary capillaries. If an animal be made to breathe in an atmosphere containing 30 per cent. of CO_2 , *absorption* of this gas by the blood is found to take place, as the pressure of the carbonic acid in the pulmonary vesicles surpasses that in the capillaries.

Other factors than the physical laws of pressure seem also to exercise their influence. If blood be shaken up with oxygen more CO_2 is disengaged than if it be agitated in a vacuum or with any other gas. The carbonic acid so eliminated is probably that which had been fixed by the red blood corpuscles, and is displaced by the oxygen (Mathieu and Urbain, Setschenow, &c.) The red corpuscles seem to contain some substance which has the power of displacing the carbonic acid : according to some (Preyer, Gaule) this substance is the hæmoglobin ; according to Hoppe-Seyler the expulsive agency is due to the presence of the fatty acids formed by its decomposition. An hypothetical acid, peculiar to lung tissue (*pneumic acid*), has been described by Robin and Verdeil as the displacing agent, but its presence has not been demonstrated, and its existence is generally disbelieved. The experiments of Müller, however, tend to show that the lung tissue has some peculiar influence in the elimination of carbonic acid.

The amount of CO_2 eliminated is influenced by various circumstances :

Age.—The amount of carbonic acid exhaled appears to increase up to 30

years of age, after which it gradually decreases. The following table from Andral and Gavarret shows the amount given off in twenty-four hours at different ages:—

Age.					Quantities of CO ₂ .
8 years	.	.	.	.	440 grammes.
15 "	.	.	.	.	765 "
16 "	.	.	.	.	949 "
18—20 "	.	.	.	.	1002 "
20—40 "	.	.	.	.	1072 "
40—60 "	.	.	.	.	887 "
60—80 "	.	.	.	.	808 "

But in proportion to the weight of the body the proportion of CO₂ eliminated is much greater in infancy and childhood than in later life. (In infancy it is nearly double.) *Sex*.—The elimination of CO₂ is greater in man than in woman. The difference is most marked about puberty, when the proportion is nearly double (Andral and Gavarret). *Constitution*.—In healthy, vigorous individuals the proportion of CO₂ exhaled is greater. *Stature*.—The elimination of CO₂, and, indeed, the general activity of respiration, is greater in individuals (including lower animals) of small stature.

Influence of the various functions.

Number of respirations.—If the number of respirations be increased while the depth remains the same, the elimination of CO₂ is also augmented, but not in proportion to the quantity of air respired.

No. of respirations.	Quantity of air expired.		Quantity of CO ₂ expired.		CO ₂ per 100 vols. of air.
12 ..	6,000	..	258	..	4.3
24 ..	12,000	..	420	..	3.5
48 ..	24,000	..	744	..	3.1
96 ..	48,000	..	1,392	..	2.9

Depth of the respirations.—If the depth of the respirations be increased while the number remain equal (12 per minute) the quantity of CO₂ exhaled is also found to increase, but not in the same proportion.

Quantity of exp. air.	CO ₂ expired.		CO ₂ per 100 vols. of air.	
500 cc. ..	21	..	4.3	
1,000 " ..	36	..	3.6	
1,500 " ..	51	..	3.4	
2,000 " ..	64	..	3.2	
3,000 " ..	72	..	2.4	

Duration of the expiratory pause.—When the respiratory movements are stopped for a certain time, the air of the lungs becomes charged more and more deeply with CO₂. This increase is at first rapid, then more slow, and also varies according to the depth of the respirations.

Duration of respiration.	Quan. of CO ₂ in exp. air (1800cc.)		Quan. of CO ₂ in exp. air (3600cc.)	
	in cent. cubes.	per 100 vols.	in cent. cubes.	per 100 vols.
20 sec.	.. 108.5	.. 6.03	.. 183	.. 5.09
25 "	.. 111.2	.. 6.18	.. —	.. —
30 "	.. 115.	.. 6.39	.. —	.. —
40 "	.. 119.	.. 6.62	.. 205	.. 5.71
50 "	.. 119.	.. 6.62	.. —	.. —
60 "	.. 120.9	.. 6.72	.. 228	.. 6.34
80 "	.. —	.. —	.. 240	.. 6.67
100 "	.. —	.. —	.. 265	.. 7.38

Alimentation.—*Inanition* diminishes the amount of CO₂ eliminated while it is increased by food, which causes increased depth of the respiratory movements, without any appreciable change in the proportion of CO₂. The increase is shown about half-an-hour after a meal, and the curve of its elevation presents two maxima, and corresponds to the curve of variation of the quantity of expired air (Vierordt).

The quantity of CO₂ eliminated also increases with the amount of carbon contained in the food. It is diminished by alcohol, tea, and coffee. Injection into the blood-vessels of substances easily oxidised (glycerine, lactates, &c.) has the effect of increasing the amount of CO₂ exhaled.

Muscular action.—Muscular exercise increases the amount of CO₂ eliminated. In an adult Pettenkofer and Voit found that 832 grammes of CO₂ were eliminated in twenty-four hours in repose, and 980 during moderate exertion. But this quantity can be enormously increased, even up to three times the amount. If tetanus of the lower limbs be artificially produced in a dog, the quantity of CO₂ expired is found to be increased. Dynamic work increases the proportion of oxygen more than static (Speck).

Sleep.—Sleep diminishes the amount of CO₂ given off. For 100 parts of CO₂ eliminated during twenty-four hours, 58 parts are exhaled during the day and 42 during the night. This difference is still greater if there has been active muscular work performed before sleep.

Menstruation.—After the menopause the exhalation of CO₂ increases for some time, after which it gradually diminishes with advancing years. *Pregnancy* increases the discharge of CO₂.

Temperature.—The elimination of CO₂ is increased by all the causes which elevate the proper temperature of the body, and diminished by whatever causes its diminution. Mathieu and Urbain found that during an elevation of temperature there was an increase of oxygen and a diminution of the carbonic acid of arterial blood, while by lowering the temperature the conditions are reversed. Lowering of the *external* temperature increases the elimination of CO₂.

Time of day.—The maximum elimination is a little after noon. From that time it diminishes till about midnight.

Light.—Light favors the exchange of gases, and, accordingly, it is found that animals placed in darkness absorb less oxygen and give off less carbonic acid than in the light (Moleschott). A similar effect has been noticed when, instead of placing an animal in obscurity, the light is prevented from reaching the retina (Pflüger, v. Platen).

Elimination of Nitrogen.

Expired air nearly always contains a little more nitrogen than inspired (Regnault and Reiset); the former containing 79.3 per cent., the latter 79.2. This would represent a daily discharge of 600cc. (7 or 8 grammes) of nitrogen. It has been referred to two sources: (a) the nitrogen of the albuminoids, either of the food or of the tissues: it has been found that when an animal is fed on a meat diet, the whole of the nitrogen taken into the system is not to be found in the urine and fæces, and the balance would be discharged by the pulmonary surface. (b) The nitrogen of the air is introduced with the food, and absorbed into the blood in passing along the alimentary canal.

This pulmonary exertion of nitrogen has been denied by Bischoff and Voit, but is confirmed by most other observers who have experimented on the subject.

Elimination of watery vapor.

About 330 grammes of watery vapor are daily eliminated from the pulmonary mucous membrane. It comes from two sources: (a) the water of the blood; (b) the water of the inspired air. The temperature of the expired air being practically constant, and the quantity of watery vapor very near the point of saturation, it follows that the proportion of watery vapor in the expired air is also constant; consequently, the quantity of water lost by the blood shall depend, *ceteris paribus*, on the hygrometric condition of the inspired air.

The *absolute quantity* of watery vapor given off from the lungs increases with the *depth* and *duration* of the respirations. The same effect is produced by cold, by dryness of the atmosphere, and by lowering of the barometric pressure.

CHAPTER XIII.

ANIMAL HEAT.

LIVING animals, with regard to their temperature, may be divided into *warm-blooded* (or, better, with blood of *constant* temperature), and *cold-blooded* (with blood of *variable* temperature). The blood of the former class of animals (mammals, birds), have a constant uniform temperature which, as a mean, oscillates between 36° and 40° C. ($96^{\circ}.8$ — 104° F.) for mammals, and 40° to 43° C. (104° — $109^{\circ}.4$ F.) for birds. This temperature is not materially affected by any changes in that of the surrounding medium. In cold-blooded animals (reptiles, amphibia, fishes), the temperature oscillates within very wide limits, following very closely that of the external medium.

The mean temperature of the human body in the axilla is a little above 98° F. (97.7 — 99.14). That of the uncovered parts of the surface, however, varies within wide limits. The temperature of the inner parts of the body is higher, and the maximum is that of the liver ($40^{\circ}.6$ — $40^{\circ}.9$ C., $105^{\circ}.08$ — $105^{\circ}.62$ F.); then of the brain, the glands, muscles, and lungs (in order). The temperature of the blood on the right side of the heart ($38^{\circ}.8$ C.), is a little higher than that of the left side of the heart ($38^{\circ}.6$ C.) (Cl. Bernard, Korner). Korner attributes this difference to the proximity of the liver on the right side, which transmitted its heat through the thin walls of the right ventricle; others have attributed the difference, and with greater probability, to the cooling process of circulating through the pulmonary capillaries. The temperature of arterial blood diminishes as it recedes from the heart. That of the venous blood is very variable, while the blood of the superficial veins is cooler than that of the corresponding arteries, the venous blood of the glands and muscles, during activity, is warmer than the arterial blood of these organs. From above the renal veins, the blood of the inferior vena cava is higher than that of the aorta at the corresponding level, and the temperature in the former

vessel increases as it approaches the heart. This change is due to the addition of the blood of the hepatic vein, which is the warmest ($39^{\circ}.7$ C.) in the body, and 1° C. higher than that of the aorta. The following are the recognised temperatures of the cavities of the body rectum, $37.5-38$; mouth, 37.19 ; vagina, $37.55-38.05$; uterus, $37.77-38.28$; external auditory meatus, $37.3-37.8$; the temperature of the stomach is lower than that of the intestine.

Sources of Heat.—The production of heat in the living body is due, (a) to chemical actions, and (b) to mechanical actions.

(a) *Chemical action.*—The chief source of the production of heat is oxidation (combustion). Whenever two atoms combine, a certain quantity of heat is set free, and the ceaseless round of chemical processes which are taking place throughout the body is in this way constantly supplying heat. The chief source of heat then is oxidation, but other forms of chemical change are continually aiding in the maintenance of an equitable temperature.

(2) *Mechanical action.*—The friction of the blood within the vessels also produces heat, but as this is directly traceable to muscular contraction (that of the heart), it may be ultimately referred to chemical action. The same observation may be applied to the friction of the articular surfaces, tendons, &c., in the movements of the skeleton.

Situations of heat-production.—It is now known that the *muscles* are the principal seat of the production of the heat of the organism. A muscle is not able to produce mechanical work without increased liberation of heat, and some go so far as to say that this is the only source of the heat of the system, and that the temperature is maintained during the time of repose by the action of the heart, and that of the inspiratory muscles.

The muscles are not, however, the sole seat of heat-production; a certain proportion appears to be set free in the *nerve-centres*. The *brain* is, after the liver, the warmest of the organs, and the blood of the lateral sinus is of higher temperature than that of the carotid artery. Similarly, in case of the *glands*, the venous blood is warmer than the arterial (Ludwig).

The lungs were believed, after the discoveries of Lavoisier, to be the great, laboratory in which the heat of the organism was set free; but this idea has long been exploded. It is true that

at the end of each inspiration a certain quantity of oxygen combines with the hæmoglobin, and, in consequence, a disengagement of heat takes place; but this is, in the ordinary condition, compensated for by the cooling produced by entrance of the external air, and by the amount of heat rendered latent in the passage of carbonic acid from the state of solution into the gaseous form.

Relation between production of heat and mechanical labor.—The mean result of the varying observations on the subject gives 2,700 calories as the quantity of heat produced by the human body in twenty-four hours. There is an intimate relation between the production of heat and that of mechanical work, as can easily be understood from the remarks we have already made. The *correlation of forces* is applicable to living organisms, as to inorganic substances; and both are governed by the laws of equivalence of heat and movement. The mechanical work of muscles, calculated in kilogrammetres, may be valued in calories; the kilogrammetres may be changed into calories on dividing by 425. A muscle is then analogous to a vapour machine which burns carbon and produces kinetic energy in the form of external work and heat; and, as in case of the machine, the wear of the metal and the production of oxide of iron are insignificant in proportion to the oxidation of carbon, the consumption of albuminoid substance in muscle is but accessory, and takes a very small share in the production of active movement. According to the calculations of Hirn, if the period of movement be compared to that of repose, we find that the production of kinetic energy (heat and mechanical work), is but doubled, while the consumption of oxygen is nearly multiplied by four (30.72 : 119.84).

The quantity of heat produced by muscular contraction would be sufficient to raise the temperature of the body $1^{\circ}.2$ C. during repose, and 5° to 6° during movement, if other causes did not intervene to prevent it. According to Davy, however, an increase of temperature of .3 to .7 may take place during muscular exercise. Privation of exercise has the opposite effect.

Distribution of heat.—The production of heat being, as we have already seen, variable in different parts of the organism, it is necessary for the maintenance of equilibrium that the

excess produced in the great centres of oxidation should be conveyed to the other parts of the body. The circulating blood is the vehicle by which the heat is conveyed, as soon as generated, to the various parts of the system. Such a mode of distribution is essential, as the tissues of the body form so bad conductors that equilibrium would otherwise be established very slowly.

The temperature of an organ accordingly depends on these three conditions: (1) the quantity of heat produced in the organ itself; (2) the quantity of heat yielded to or taken up by the organ from the circulating blood; (3) the temperature of the surrounding organs and their conductivity.

Loss of heat.—As the organism is continually producing heat, the temperature would be gradually elevated to an indefinite degree, if the loss of caloric did not proceed in the same proportion. This dispersion of heat takes place in different ways. The greater proportion is lost by radiation from the cutaneous surface; another portion is lost in heating the inspired air and the ingesta; a third part disappears in the evaporation of water, exhaled from the pulmonary and cutaneous surfaces.

The following table gives the percentages of the heat of the organism which are spent in the different ways mentioned:

Skin 87.5	{	Radiation	73.0	}	21.7
		Evaporation	14.5		
Lungs 10.7	{	Evaporation	7.2		
		Warming the inspired air	3.5		
Warming the ingesta			1.8		
			100.0		

The conditions which govern the loss of heat are to be found: on one part in the organism; on the other, in the external medium (for man, principally the atmosphere). On the side of the organism the skin plays the most important part; the epidermis, which is a bad conductor, is opposed to a rapid loss, and the presence of the cutaneous secretion has a still more powerful influence, as the increased activity of its evaporation is accompanied by an increased expenditure of heat.

The air is a bad conductor of heat, but its temperature and humidity directly influence the loss of heat, by favoring or

retarding radiation and evaporation. The movement of the surrounding air has, from this point of view, the greatest importance. When the layers of air in contact with the surface are continually changing, there is a rapid loss of heat by radiation and evaporation in consequence (supposing that the temperature of the air is below that of the body). On the other hand, when a layer of atmospheric air is kept in contact with the surface (which is the effect of clothing), the loss of heat is much less rapid.

Equilibrium between the loss and the production of heat.—This balance is affected (a) by the variations in the production of heat, and (b) by the variations in its expenditure. The variations of production depend on the activity of the great seats of combustion (muscles, brain, glands, &c.); the variations in expenditure, on the other hand, depend either on the organism, the external medium, or the nervous system, which forms the connecting link between. The latter indeed is, as we shall see later on, the true regulator of animal heat, as the blood is the distributor.

(1) The mean temperature is increased :—

(a) By increased production of heat without any change of expenditure.

(b) By diminution of expenditure without change of production.

(c) By increase of production and diminution of expenditure.

(d) By increase of production and insufficient increase of expenditure.

(e) By diminution of expenditure and diminution of the production of heat, if the first is greater than the second.

(2) The mean temperature is diminished in the contrary cases. An increased production of heat co-exists with—

(a) An increase of the mean temperature, if the loss of heat is unchanged.

(b) Maintenance of the mean temperature, if the loss increases.

(c) Lowering of the mean temperature, if the loss is very great.

Similarly, an increased expenditure of heat accompanies :—

(a) A diminution of the mean temperature, if the production does not increase.

(b) Maintenance of the temperature, if the production of heat is increased.

(c) An augmentation of the mean temperature, if the production of heat is more considerable.

When a sudden subtraction of heat occurs (as by use of a cold douche), an immediate *increase* of temperature results (Liebermeister, Hoppe).

Influence of the nervous system.—The nervous system, espe-

cially the vaso-motor part, is the true regulator of the heat of the system. Section of the cervical sympathetic was found by Cl. Bernard to produce vascular dilation, and increase of temperature on that side. Section of the vaso-motor nerves in other parts of the body is followed by a similar result. Stimulation of these fibres, on the other hand, produces a lowering of the temperature of the part corresponding to their distribution. The action of these nerve-fibres is double, (*a*) they influence the *production* of heat, by causing capillary dilation, and consequent increase of oxidation, and so elevating the temperature; and (*b*) they influence the *loss* of heat, for when the vessels of the skin are dilated, the loss of heat is greater by radiation, by evaporation, or by both.

Section of the spinal cord is followed by a lowering of temperature, which gradually increases till death (Cl. Bernard, Schiff, Brodie). This result is probably due to division of the vaso-motor fibres contained in the cord, causing dilation of the cutaneous vessels, so as to increase the loss of heat. If the animal be placed in a heated oven there is, on the contrary, an increase of temperature (Billroth, Weber). According to Parnaud, however, there is also a diminution of oxidation in the paralysed parts. Stimulation of sensory nerves (auricular, sciatic), causes a lowering of temperature (Hood).

Variations of the temperature of the body—Age.—The temperature of the fœtus (still in utero), was found by René to be $37^{\circ}.91$ C. After birth it is $37^{\circ}.81$; within the first few hours it falls to 37° , and during the next ten days it re-ascends ($37^{\circ}.2$ — $37^{\circ}.6$). The axillary temperature immediately after birth was, in the majority of cases, greater than that of the rectum—the difference being sometimes up to 1° C. The temperature retains the same height from the first few days after birth up to puberty; it then declines up to the age of fifty, when it attains the minimum, after which it re-ascends in old age. *Sex.*—The influence of sex is barely perceptible; it appears a little higher in the female. *Alimentation.*—A slight rise is generally admitted to exist after ingestion of food ($0^{\circ}.6$ C.), but this may not take place, and Vintschgau and Dieft have reported a fall (observed in dogs with gastric fistulæ). R. Maly has observed an absorption of heat in the artificial digestion of albuminoids and hydrocarbons, which would explain the slight chill experienced after meals. *Muscular exercise.*—According to J. Davy the temperature ascends during muscular exercise, especially in warm climates (about 1° C. under the tongue). This also occurs in severe *mental work*, but to a less amount. *Sleep* has little influence. *Menstruation* and *pregnancy* (except in the last two months), do not affect the temperature, except by causing a slight increase. After *death*, before the rigor mortis is established, a slight elevation of temperature has been observed; this is probably due, in part, to the diminished

loss of heat caused by arrest of the circulation, and, in part, to an increased production (coagulation of blood, coagulation of myosin, continuation of chemical changes).

Variations due to external causes.—The *temperature* of the external media has a considerable influence over that of the body, partly from its physical effects, and partly from its action on the nervous system. *Season.*—The temperature is a little higher in winter than in summer ($0^{\circ}.1-0^{\circ}.2$ C). The influence of climate is analogous (Davy, Brown Sequard). *Toxic influences.*—A lowering of temperature is caused by anæsthetics, alcohol, digitalis, nicotin, curara, &c.

CHAPTER XIV.

NUTRITION.

IN order to maintain the phenomena of life and health it is necessary that a quantity of nutritive matter must be supplied which exactly compensates for the losses sustained by the organism. The following tables, drawn up by Vierordt, give the balance of the gain and loss of the system during twenty-four hours. This arrangement is more or less theoretical and artificial, but such an equilibrium must, of course, be continuously maintained, whatever may be the variations which it undergoes:—

I.—INGESTA.

	Total.	C	H	N	O
Oxygen inspired ..	744.1	—	—	—	744.11
Albuminoids ..	120	64.18	8.60	18.88	28.34
Fats ..	90	70.20	10.26	—	9.54
Starch ..	330	146.82	20.33	—	162.85
Water ..	2818	—	—	—	—
Salts ..	32	—	—	—	—
	4134.1	281.20	39.19	18.88	944.84

II.—EGESTA.

	Total.	H ₂ O	C	H	N	O	Salts.
Respiration ..	1229.9	330	248.8	—	?	651.15	—
Skin.. ..	669.8	660	2.6	—	—	7.2	—
Urine ..	1766.0	1700	6.8	2.3	15.8	9.1	26
			3.0	1.0		2.0	
Fæces ..	172.0	128	20.0	3.0	3.0	12.0	6
Water (formed in the organism) ..	296.3	—	—	32.89	—	263.41	
	4134	2818	281.2	39.19	18.8	944.8	32

According to the first table the nitrogenous are to the non-nitrogenous principles of food as 1 : 3½, and we know that this ratio is nearly preserved in the well-regulated dietary of an adult. The second table gives the following percentage of the substances eliminated by the different organs: respiration, 32; skin, 17; urine, 46.5; fæces, 4.5.

In most cases the total quantity of nitrogen taken into the system is not represented by the quantity eliminated in the fæces and urine. The deficit is supplied by the external air, the sweat, and other epidermic products.

Inanition.—When aliments are completely cut off the substance of the organism is gradually consumed; disassimilation continues in the tissues and organs, and they have no other source for repair than that supplied by the blood. This fluid, however, having ceased to receive any new products of digestion, soon ceases to furnish to the tissues the materials necessary for their nutrition. When the moment arrives at which disassimilation goes on without any assimilation, the body begins to lose weight. The loss of weight is, however, of different proportion in the different organs; in the tissues of which the nutrition is very active it progresses rapidly, and slowly under the opposite conditions. Two other conditions also intervene; the chemical composition of the tissue itself, and the nature of the reparatory principles which it has to take from the blood. On this account the fat disappears rapidly from the system, being very oxidisable, and partly from the fact that the proportion of fat contained in the blood is insufficient to supply the material of repair for any length of time. The albuminoid tissues, on the other hand, waste more slowly, their oxidation being more tardy, and the material of supply from the blood-serum very considerable. The blood is, accordingly, the first to suffer from inanition; it diminishes in quantity, becomes concentrated, and loses its albumen; and the number of red corpuscles diminishes, but their proportion, and that of the fibrin, do not sensibly vary. The following tables from Chossat and Voit give the percentage of loss of weight for the different organs at the end of inanition.

			Chossat.		Voit.
Fat	-	-	93.3	-	97.0
Blood	-	-	75.0	-	27.0
Spleen	-	-	71.4	-	66.7
Pancreas	-	-	64.1	-	50.0

			Chossat.		Voit.
Liver	-	-	52.0	-	53.7
Heart	-	-	44.8	-	32.6
Muscles	-	-	42.3	-	30.5
Kidneys	-	-	31.9	-	25.9
Bones	-	-	16.7	-	13.9
Nervous centres	-	-	1.9	-	9.2

During the progress of inanition the secretions diminish in quantity, and become more concentrated ; the urine is strongly acid, even in the herbivora, and the proportion of urea diminishes, at first rapidly, then more slowly, till death. The respiratory changes also diminish in activity ; less oxygen is absorbed, and less carbonic acid eliminated. The temperature at the same time falls ; according to Chossat the fall is $0^{\circ}.3$ C. per diem for warm-blooded animals ; the respirations and pulse at the same time diminish in frequency, and every form of muscular activity loses its energy. Innervation is least affected, and the brain is, of all the organs, that which loses least weight. Death takes place after a period of time which varies in the different species, and for individual conditions ; in the case of man, we have hardly sufficient data to determine a medium. In birds and small mammals it generally happens at the end of about nine days ; it occurs sooner in young animals, and more slowly when a large quantity of fat is present. In cold-blooded animals, inanition can be supported for a very much longer time ; frogs, it is said, have been kept alive for nine months without food.

Origin of the Constituent Principles of the Tissues.

The ultimate constituents of the tissues may be divided into three classes, corresponding to the three groups of simple aliments : albuminoids, fats, and hydrocarbons. They are all supplied by the plasma of the blood, which is continually transuding through the capillary walls, and bathing the various tissues.

Albuminoids.—These come exclusively from the albuminoids of the food. The theory usually accepted is, that the latter are changed into peptones in the alimentary canal, and passing into the blood as such, are there changed by some unknown process into serum-albumin. A different theory has, however, been recently advanced by Fick. We have already mentioned the idea of Brücke and some other physiologists, who assert that a portion of the albumin is absorbed without change, while another portion is absorbed after being changed into peptone. According to Fick, it is the

unchanged albumin so absorbed which alone serves for the repair of the tissues, and the formation of the albuminoid substances of the organism. The peptones are, he supposes, destroyed in the blood, and by their decomposition form various products of excretion, azotised (urea), and non-azotised. If peptones be injected into the veins of an animal, all the nitrogen will be found in the urine after some hours. He also lays great stress on the fact that, after a meal of animal food the increase of urea (to ten or twelve times the proportion before food) can only be explained by attributing the production of urea to a direct change of the peptones absorbed from the digestive tube.

The albumin of the liquor sanguinis undoubtedly furnishes the albuminoid substances of the tissues, myosin, keratin, elastin, &c., but the exact nature of the transition still remains a mystery. The proportions of sulphur, carbon, and nitrogen in these substances differs from that in albumin, properly so called; and none of them have been produced artificially, although Rochleder at one time believed that he had obtained chondrin by heating albumin with hydrochloric acid (air being excluded during the process).

Fats.—The mode of formation of fats is extremely obscure, and the part taken in the production by the chief groups of aliments is still undetermined. (a) *Fats.*—That the fats ingested enter into the formation of the fats of the tissues is too obvious to be doubted; even allowing that a portion is oxidised immediately without entering into the constitution of the tissues. But what the exact nature of the intermediate changes may be, which the fats absorbed as such, as well as those absorbed in the form of soaps, have to undergo before they come to form a part of the anatomical elements, is entirely unknown to us up to the present. (b) *Hydrocarbons.*—According to Liebig, a portion of the hydrocarbons ingested are oxidised, and the remainder changed into fatty tissue. In favor of this idea would be the facts that lean carnivorous animals quickly fatten when hydrocarbons are added to their food, and that bees, whose food is almost purely saccharine, produce wax, which is closely allied to fatty substances. Against this view, however, we know that the hydrocarbons, when taken alone, diminish, instead of increasing the fats of the organism; and if albuminoids are completely wanting from the food of bees, leaving a purely saccharine alimentation, the production of wax is arrested. In order to reconcile the apparent discrepancy of these facts, Voit has suggested what appears to be the most probable explanation: the hydrocarbons do not contribute directly to the formation of fats, but do so indirectly by their property of easy oxidation; they diminish the consumption of the fats obtained from other sources, and in this way preserve them in the body. (c) *Albuminoids.*—The production of fats from albuminoids, an idea first advanced by Boussingault, is now generally accepted by physiologists. Kemmerich has observed a formation of fat at the expense of the casein in milk exposed to the air. The formation of adipocire from the albuminous tissues in dead bodies is also in favor of this view. It is a well-known fact, that in animals, during lactation, the use of nitrogenous food increases the fat of the milk, which, on the other hand, diminishes with the use of a saccharine or amylaceous diet.

SECRETION.

Secretion is the peculiar process by which substances are separated from the blood, either for the purpose of fulfilling some useful function in the animal economy, or to be cast off as excrementitious matter. In the former case, they are the *secretions*, properly so called; in the latter case, they are more correctly known as *excretions*.

The simplest form of secreting organs are found in the membranes: *serous*, *synovial*, and *mucous*, the surfaces of which are continually moistened by a fluid which is formed by the epithelial cells on the surface. The *serous membranes* form shut sacs, which are doubly folded on the organs which they invest, and, by the smoothness of their surfaces, allow free gliding motion. Their surfaces are covered with a single layer of flattened, polygonal, endothelial cells, with a basement layer formed by a meshwork of bundles of white and yellow fibres, closely felted in many situations, so as to form a *fenestrated membrane*. Here and there, on the surface of the membrane, are minute openings (*stomata*), which pass directly into the lymphatics. Around these openings the cells are somewhat cubical in form with granular contents.

The *synovial membranes* are found in the interior of joints, and present some points of resemblance to the serous membranes. They differ in general form from the latter, and they make but a tubular lining for the ligaments of each joint, instead of closed sacs, as was formerly asserted by some. They are not prolonged over the encrusting cartilage, but terminate in a vascular fringe (*circulus articuli vasculosus* of W. Hunter).

The *mucous membranes* are described at sufficient length in connection with the various tubes which they line. Collectively regarded, they form two great tracts: the *gastro-pulmonary* and *genito-urinary*.

The several fluids formed by these membranes present each their own peculiarities. The serous fluid which moistens their cavities differs but little, if at all, from dilute liquor sanguinis. The synovial fluid, which lubricates the interior of joints, differs from it markedly, by its greater density and viscosity, and in the large proportion of albumin contained.

The organs specially set apart for the purposes of secretion

are known as the *secreting glands*. They all present some peculiar modifications of structure, especially in the form and arrangement of their cells. There are two chief varieties: the *tubular* and the *racemose*. Of the first there are two kinds: the *simple* and the *compound*. The former are more or less regularly cylindrical pits, which are lined with epithelial secreting cells. The latter differ in branching in a more or less complex manner, the terminal subdivision being generally convoluted. The *racemose* glands branch in a very complex manner, and, at the termination, each branch expands and forms a dilatation. This saccular expansion (known as the *acinus*) is lined by a peculiar form of columnar cells, generally somewhat spheroidal in shape, and resting on a basement membrane, formed by an even layer of homogeneous cell-plates, and surrounded by a lymph-space, outside which is a plexus of capillary blood-vessels. The glands are freely supplied by nerves, and Pflüger's peculiar views of the connection of the terminal twigs of the nerves with the epithelial cells has been already noticed.

CHAPTER XV.

THE VASCULAR (DUCTLESS) GLANDS.

UNDER this name is comprehended the thymus, thyroid body, spleen, and supra-renal capsules ; the pineal, Pacchionian, and pituitary bodies ; the coccygeal and intercarotid glands. Some would also include the tonsils ; and the solitary and agminated glands of the intestine, as well as the lymphatic glands, are allied to this group. These structures have no ducts, and the products of their activity are added directly to the circulation.

Thymus.—This body is invested by a capsule of fibrous tissue, which sends a number of septa into the interior of the organ, dividing its substance into lobes and lobules. These septa contain the blood-vessels and lymphatics. The capsule is invested by a process of the pleura.

Microscopically examined, the gland is found to be made up of follicles of irregularly polyhedral or cylindroid shape, and consisting of cortical and medullary portions, of which the former is usually larger in quantity. The matrix of the follicles consists of a fine reticulum, formed by nucleated branched corpuscles, the processes of which form a meshwork by their communication, in the interstices of which lymphoid corpuscles are placed. These corpuscles are more numerous in the cortical than in the medullary portion of the follicles, and consist each of a delicate layer of protoplasm, enclosing a spherical nucleus. Large, transparent endothelial cells are also found in the meshwork of the reticulum, and, being more numerous in the medullary portion, cause the greater transparency of this region of the follicle. They usually contain a single nucleus, but some large ones are found, of granular aspect, which contain two or three nuclei (*large granular cells* of Watney). *Concentric corpuscles* are found in the medulla, each formed by a granular nucleated mass, around which flattened cells are arranged in a more or less concentric form.

Each follicle presents a network of capillary blood-vessels, and is more or less completely surrounded by a lymph-space.

The functions of the thymus are supposed to be nearly, if not quite, identical with those of a lymphatic gland; but the question is still very obscure.

Thyroid body.—As in case of the thymus, this body is surrounded by a fibrous capsule, which sends septa into the interior, dividing its structure into lobes and lobules. The subdivision of the interlobular septa gives rise to the formation of a mesh-work, in which lie the *alveoli* or *vesicles*, which make up the characteristic gland-structure. The alveoli are more or less regularly spheroidal in shape; some appear tubular or branched, especially in the growing structure.

Each alveolus is invested by a *membrana propria*, formed by a single layer of flattened cells: this is lined by columnar epithelial cells, which are developed originally from solid cylindrical prolongations of the hypoblastic epithelium of the adjacent part of the foregut (Baber). The trabecular processes of connective tissue are derived from the mesoblast, and, stretching inwards from without, come to intersect these cylindrical masses, and divide them into segments, which become rounded off into the alveoli of the mature body. The interior of each contains a homogeneous, viscid, semi-fluid substance, of a slightly yellowish tinge. Numbers of blood-corpuscles, both colored and colorless, are also found within the alveoli in the various stages of degeneration, and some nucleated cells from inter-alveolar connective tissue (*parenchymatous cells* of Baber).

The *blood-vessels* and *lymphatics* ramify in the interalveolar connective tissue, and the alveoli are, more or less, completely surrounded by lymph-spaces, which communicate with the open mouths of the latter. The lymphatics contain a viscid, semi-fluid, transparent substance, identical with the contents of the alveoli (Baber).

The viscid contents of the alveoli seem to break up the blood-corpuscles which pass into their interior, by a process analogous to maceration (Klein).

Spleen.—The spleen is covered by a layer of endothelial cells continuous with those of the peritoneum, which covers a connective-tissue membrane, abounding in elastic fibrils. Beneath this is the proper capsule of the organ, formed of folded connective-tissue fibrils, which interlace in all directions, and also

contains delicate bundles of smooth muscle cells (W. Müller, Kyber), arranged in the form of a fine plexus. Passing into the interior of the organ from its capsule are bundles of connective fibres, which, intersecting in all directions, form a meshwork throughout its substance; a considerable amount of unstriped muscular tissue is also present (W. Müller, Meissner, &c.). Some branches of the trabeculæ terminate in free extremities in the parenchyma (Klein).

The enclosed parenchyma consists of the *Malpighian corpuscles* and the *spleen pulp*.

The branches of the splenic artery enter the organ at the hilum, and passing along the trabeculæ, soon separate from those of the vein which first accompany them, and give off their branches at very acute angles. The larger divisions of the artery are surrounded by lymph-spaces, but this investment is replaced, in case of the small branches, by a solid tube of adenoid tissue. The wall of this tube is of very variable thickness, and swells out in places into oval or cylindrical enlargements, which are generally known as the *Malpighian corpuscles*. Accordingly, "it is incorrect to describe the Malpighian corpuscles, as is occasionally done, viz., as isolated spherical or oval masses of adenoid tissue" (Klein).

The *pulp* is made up of a matrix of flattened endotheloid cells, which send off processes to interlace with those of neighboring cells, and form a meshwork in which lymphoid corpuscles are imbedded. Both the endotheloid and the lymphoid corpuscles sometimes contain colored blood-corpuscles in variable quantity, as was first pointed out by Kölliker. This is not always seen in the human spleen. The lymphoid corpuscles are sometimes connected to the other cells by a shorter or longer stalk, and from this circumstance it has been considered "probable that they are developed from them by a process of gemmation."

The arteries ultimately form capillary branches, which pass to the Malpighian corpuscles, and at the margins of the latter open into the spaces of the pulp-tissue. These on the other side lead into the open mouths of venous sinuses (*cavernous veins* of Billroth), which form elongated plexuses, in the meshes of which lie the *intervascular tracts* of Billroth. According to Billroth, Frey, Klein, and others, these tracts contain no capillaries, and the only communication between the arterioles and

the venous sinuses lies through the honeycombed spaces of the matrix.

The *lymphatics*, as already mentioned, accompany the blood-vessels in the trabeculæ, and form, in some places tubular vessels, in others a network of intercommunicating lymph-spaces. They form a rich plexus in the capsule, but do not extend into the trabeculæ.

The *nerves* of the spleen are non-medullated fibres, which accompany the arteries, and seem to terminate in the arterio-capillary sheaths.

The functions of the spleen have long been a source of discussion, but are, even up to the present, largely involved in obscurity. There can be no doubt, however, that it exercises a very active part in nutrition and blood-formation.

The *volume* of the spleen undergoes rapid modifications from time to time according to the condition of the circulation and the influence of the nervous system. This is accounted for by its great vascularity and the abundance of elastic tissue (with smooth muscle cells) which is present in the capsule and trabeculæ. If the nerves are divided at the hilum before entering the organ, it expands enormously, because of the removal of the influence of the unstriated muscle tissue which regulates the calibre of the blood-vessels; if the artery be tied without including the plexus, no enlargement takes place; if the artery and plexus are tied together, the organ swells by the venous regurgitation (A. Moreau).

The spleen is also *contractile*, and its contractility is under the influence of the nervous system. The size of the organ diminishes during stimulation of the left sympathetic trunk, or its greater splanchnic branch, also during stimulation of the solar or splenic plexus, semilunar ganglion, upper part of spinal cord, medulla oblongata, or cortex cerebri. Electric stimulation of the skin over the splenic region has been found to produce the same result in man. Reflex contraction follows stimulation of the central end of the divided pneumogastric, of the superior laryngeal, or of sensory nerves, such as the sciatic or median. Nausea, vomiting, or asphyxia have a similar effect. Contraction of the spleen is also produced by quinine, strychnine, camphor, eucalyptus, ergot of rye (?), and by cold water. Curara antagonises the action of these agents (Bulgak).

During digestion the spleen expands, and the maximum (in case of the rabbit) is attained five hours after eating (Schönfeld).

The splenic venous blood contains more white corpuscles than the arterial, but the exact proportion has been very differently reported. It is also less coagulable, although it was found to contain more fibrin by Beclard and Gray; this has, however, been denied by other authorities (Fünke, Estor, Saint-Pierre).

The chemical composition of the spleen is very peculiar. It contains in 1,000 parts: of water, 775; organic matters, 180-300; ash, 5-9.5 (Oidtmann). Among the organic matters are found: leucin, tyrosin (?), xanthin, hypoxanthin, taurin, uric acid, also acetic, butyric, formic, lactic, and succinic acids; inosit, cholesterin. A peculiarity in its composition is the large proportion of iron and potassium which is present.

Extirpation of the spleen, which has been practised with success on man and animals, has not given any definite results; the probable cause, however, is that the other lymphoid organs supply its functions. Mosler has reported a diminution of white corpuscles. Hypertrophy of the lymphatic glands has been seen in some cases; excretion of urea is increased (Friedleben); the solids of the blood diminish (Becquerel and Rodier); the iron also decreases (Maggiorani); but it is allowed by all observers that the general health remains unaffected. According to Picard and Malassez, however, it is only in youth that the operation can be done with impunity; it is fatal in old age. These observers have found transitory diminution of the red corpuscles and of the hæmoglobin in all cases. Stinstra affirms, indeed, that animals fatten more rapidly after extirpation of the spleen.

The following functions have been attributed to the spleen:—

- (1) *The formation of white blood-corpuscles;*
- (2) *The formation of red corpuscles,* or, rather, the transformation of white corpuscles into red (Schönfeld, Kölliker, Fünke). In favor of this idea, we have the fact that corpuscles exist apparently of an intermediate form between white and red; also that the venous blood of a spleen dilated after section of its nerves is richer in red corpuscles and hæmoglobin than is the arterial (Picard, Malassez). An increase of

corpuscles and of hæmoglobin also has been observed to take place in isolated places of the spleen.

(3) That the spleen is a seat of *destruction of red corpuscles* was first pointed out by Kölliker, and is now almost universally admitted by physiologists. The idea is based chiefly on observation of the cells (already mentioned) in the spleen-pulp, which contain in their interior red blood-corpuscles in various stages of degeneration.

(4) The idea that the spleen *forms the albuminoid ferment of the pancreatic juice* (Schiff's theory) has been already mentioned.

(5) Its influence on the *formation of urea* shall be referred to later on.

(6) *A reservoir of albuminoids.*

(7) The spleen has been supposed to act the part of a *diverticulum for the abdominal circulation*, especially for that of the liver and stomach (Gray, Longet, &c.) Enlargement and congestion of the liver were found to be produced by the contraction of the spleen which followed stimulation of its nerves (Drosdoff, Botscheschkarow).

Supra-renal capsules.—The functions of the supra-renal bodies are extremely obscure. The structure, which is also complex, is divisible into a cortical and a medullary portion. The cortical substance is sub-divided into three zones: an outer (*zona glomerulosa*), middle (*zona fasciculata*), and inner (*zona reticularis*).

The organ is surrounded by a fibrous capsule, which contains numerous elastic fibres, and, in the deepest portion, a layer of unstriped muscle-cells. Trabecular processes pass from the capsule, which form a reticulum through the whole substance of the organ. In the *zona glomerulosa*, the bundles are thick and the reticular spaces small; in the *zona fasciculata*, the spaces are longer, and separated by more delicate trabeculæ, while the reticular zone presents again a dense plexus, with small uniform meshes (Klein). The meshes of the *zona fasciculata* contain each a cylindrical packet of polyhedral cells; the meshes of the other zones also contain cell-masses, of less regular shape, which communicate with those of neighboring spaces.

The spaces of the *medulla* also contain anastomosing bundles of columnar or polyhedral cells, which are continuous with those of the inner zone of the cortex.

The medulla is also very rich in capillary *blood-vessels*, which form a dense meshwork. In the cortical portion the blood-vessels accompany the trabeculæ, and form corresponding meshworks.

The *lymphatics* commence in the intercellular spaces of the trabecular meshwork, in the various parts of the organ; and from the open mouths which are found here, they pass with the blood-vessels towards the capsule.

The *nerves* (derived from the sympathetic) are very abundant. The fibres are of the non-medullated variety, and form rich plexus in the medulla (Klein). In connection with these are ganglion cells; some isolated, some in groups (Holm, Eberth).

The *functions* of the suprarenal bodies still remain a puzzle to physiologists. Their intimate connection with the sympathetic has led some to believe them to be ganglionic structures belonging to the sympathetic system, but this supposition has not been substantiated. Extirpation has usually been followed by death, due probably to the severity of the operation. According to Brown-Sequard, when an animal survives after their removal, there is an accumulation of pigment in the blood. In the so-called *morbus Addisonii*, which is characterised by pigmentation of the skin, giving it the characteristic *bronze* tint, disease of the suprarenal bodies is usually, but not invariably, present.

The *pituitary body* (*hypophysis cerebri*) possesses but little physiological interest, as its functions are entirely unknown. It consists of two lobes, an anterior (larger), which is originally derived from an invaginated process of the cutaneous surface. The involution takes place in early foetal life, from the epiblastic layer; and the portion which passes in at the base of the skull is nipped off by the ossification of the bones. The posterior lobe, which is smaller and spheroidal in shape, is imbedded in a hollow on the posterior surface of the anterior lobe. The latter is a direct process of the cerebral mass, to which it is connected by means of the infundibulum.

The anterior lobe is invested by a fibrous capsule, which sends trabecular processes to intersect the interior in every direction. These form delicate lamellæ, which enclose spheroidal or cylindrical spaces, each lined by a layer of endothelial cells. Each alveolar space is occupied by one or

more branched nucleated corpuscles, which fill the space left between the lining epithelial cells.

The small posterior lobe is part of the brain substance, to which it is directly connected by means of the *infundibulum*.

The **pineal** and **Pacchionian** bodies do not require special description. The former is made up of nervous tissue, with reticular spaces in the interior, containing small calcareous masses (*acervulus cerebri*). The latter structures are generally admitted to be formed by an exuberant multiplication of the plasma cells of the connective tissue, and are placed at the mouths of the veins which open into the superior longitudinal sinus. The idea of Pacchioni, that they were secreting glands, has long been abandoned by histologists.

Glandula coccygea.—The coccygeal gland (*steissdrüse*) of Luschka, is looked upon since Luschka's discovery as one of the ductless glands. It consists of a fibrous capsule, which sends trabecular processes into the interior, dividing the body into a system of communicating spaces. A few unstriped muscle cells are found in the capsule and septa. The spaces are occupied by masses of polyhedral cells of spherical or cylindroid outline (the *gland-vesicles* and *gland-tubes* of Luschka). The cells are polyhedral in form, and, according to Luschka, are ciliated at the time of birth. The axis of each of these cell-masses is formed by a capillary *blood-vessel*. The course of the *lymphatics* is not known. The nervous supply is rich, and formed by non-medullated fibres from the sympathetic system. They have special bud-like terminations, similar to Pacinian corpuscles, according to Luschka, who has also described ganglion cells connected with the plexus which the fibres form in the stroma. The existence of both these structures has, however, been denied by Krause, and others.

The **glandula carotica** of Luschka (*ganglion intercaroticum* of older writers) presents a structure similar to that of the body just described.

CHAPTER XVI.

THE SECRETING ORGANS.

THE SKIN AND ITS FUNCTIONS.

THE skin consists of two layers; the outer protective portion, which is called the *epidermis*, *scarf-skin*, or *cuticle*, and the deeper and stronger layer, known as the *cutis vera*, *corium*, or *derma*. Certain structures, formed of modified epidermis—the *hairs* and *nails*—are usually known as appendages of the skin, and aid in the fulfilment of its functions. Within and beneath the true skin are also glandular and other modified structures, which shall be described as we proceed.

Epidermis.—The most recent histologists divide the cuticle into four strata, distinguished by the peculiarities of their cells:—

(1) *Stratum corneum*, formed of superimposed layers of scales, possessing little vitality, and continually dropping off from the surface, or removed by friction. The varying thickness of the cuticle in different parts of the body is chiefly due to the variations in this layer.

(2) *Stratum lucidum* (Schrön). This layer consists of flattened cells, so closely arranged as to form an almost homogeneous membrane. In some of the cells a nucleus can be seen.

(3) *Stratum granulosum* (Unna), or *granular layer* of Langerhans, is formed of a single layer of fusiform cells, the long axes of which are placed parallel to the surface. Each has a well-marked nucleus, and a number of granules around.

(4) *Rete Malpighii* (*vel mucosum*), the deepest layer, consists of numerous strata of cells, of which the superficial is formed of somewhat flattened cells, and the deepest layer of columnar; while the intermediate strata are composed of polyhedral cells. The deeper surface of the rete mucosum is moulded on the papillary layer of the true skin, its interpapillary processes passing down between the papillæ of the corium. The component cells give off processes from their various angles, which meet those of the neighbouring cells, and in this way limit areolar spaces through which the plasma of the blood trickles for the maintenance of their nutrition. They are known as the *prickle cells* of

Max Schultze, who first pointed out the peculiarity. The pigment, on which the varying tints of the skin is due, is found in the deeper cells of this layer. The thickness of the rete mucosum is very constant, not varying much in the different parts of the body. The basal portion of the columnar layers of cells, which is in contact with the surface of the true skin, forms the *basement membrane* (Klein).

Cutis vera.—The cutis vera is divisible into two layers—the superficial, or *papillary*, and the deep, or *fibrous*. The papillæ are conical processes of the corium, sometimes terminating by a single apex (*simple* papillæ), some divided at the extremity (*compound* papillæ). They are most numerous and prominent in the palms of the hand, palmar surface of the fingers, and soles of the feet. Their length in these situations reaches to about $\frac{1}{16}$ of an inch. In these situations they are arranged in double rows, forming parallel curved ridges, which are plainly discernible on the hand and fingers. They are smallest and most sparsely distributed on the face, where they are sometimes scarcely perceptible. On other parts of the surface they are also more or less thinly scattered. Two kinds are recognizable: the *vascular* and the *nervous*. The former contain a rich plexus of blood vessels, the latter a terminal nerve fibre.

The deeper (*fibrous*) layer of the true skin is formed by a network of fasciculi of white and yellow fibres, the latter existing in considerable proportion. The meshwork so formed is coarse in the deeper layers with wide spaces, which pass without any special boundary line into the subcutaneous areolar tissue. The superficial layers form a finely-felted network, which resembles, when freshly examined, a homogeneous membrane, the *basement membrane* of Todd and Bowman.

The blood-vessels of the skin are numerous, and its whole substance is extremely vascular, from the presence of dense capillary plexuses.

The skin is abundantly supplied with nerves, which present several peculiar terminations in its substance. Fine branching fibres have been traced into the rete mucosum, between the cells of which they terminate, either in free bulbous ends, or in fine plexuses. The special terminal nerve structures, which have been described in the true skin, are: the *Pacinian corpuscles*, the *touch corpuscles*, and the *end-bulbs*.

The **Pacinian corpuscles**, or *corpuscles of Vater* (who first described them), are somewhat oval bodies which are found mostly on the digital nerves. Each is about a line in length, and is formed by a series of concentric homogeneous capsules, about sixty in number, enclosing in the centre the termination of a nerve fibre. Each corpuscle is connected with a medullated nerve fibre, which loses its medullary sheath at the point where it enters the central clear substance (*core*) of the Pacinian corpuscle. At the same point it loses the sheath of Schwann, while the nerve-sheath is seen to be continuous with the external capsules. Each of the latter is lined by a layer of endothelial cells (Hoyer), which break down soon after death, forming the stratum of fluid, described by the old histologists, as separating the adjacent capsules. Near the distal part of the core the axis-cylinder divides into two or more branches, each of which terminates in a bulbous enlargement (*terminal bud* of Axel Key and Retzius). The substance of each of these buds is found to be a delicate network, formed by the interlacing of the primitive fibrillæ of the axis-cylinder (Grandry). The core is imbedded in a homogeneous or slightly striated matrix, and enclosed by a delicate limiting membrane.

In the mesentery of the cat beautiful specimens of these structures are found, of regularly oval shape.

The **end-bulbs** of Krause are found in the deeper layers of the ocular conjunctiva, especially near the margin of the cornea. They are spherical or elliptical in shape, about $\frac{1}{8}$ to $\frac{1}{10}$ of an inch in diameter, and surrounded each by a homogeneous capsule, which is continuous with the sheath of the nerve connected with it. The latter is a medullated fibre, which loses the medullary sheath, either before or after piercing the capsule. The interior of the latter is filled by a homogeneous or faintly striated mass, in which the axis-cylinder ends, after dividing into two or more branches, which often present bulbous extremities.

Similar structures are found in the buccal mucous membrane, and in the skin of the glans penis and glans clitoridis. In the latter situations they are more deeply placed.

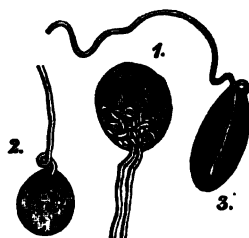


Fig. 61.

End-bulbs (after Krause), showing the different modes of termination of the nerve-fibres.

The **corpuscula tactus**, to which the names of Wagner and Meissner are attached, are found in the papillæ of the hands and feet. They are of an oval cylindrical shape, the long axis being about $\frac{1}{300}$ of an inch, and the transverse measurement about $\frac{1}{600}$. The enclosing capsule is continuous with the sheath of the nerve fibre, and presents on its inner surface a number of flattened cells, placed transversely to the long axis of the corpuscle. A medullated nerve-fibre enters the corpuscle, and winds around two or three times, in contact with its capsule. The exact mode of termination is not definitely known.

Some tactile corpuscles are also found in the skin of the palmer surface of the fore-arm and of the nipple.

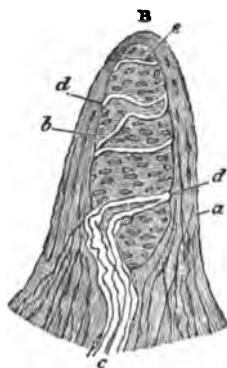


Fig. 6a.

Papilla from skin of hand, showing tactile corpuscle (Kölliker)—*a*, central layer, with cells and pure elastic filaments; *b*, tactile corpuscle, with transverse nuclei; *c*, nerve-fibre, with neurilemma; *d*, nerve-fibres winding round the corpuscle.—X 350.

Glands.—The cutaneous glands are of two kinds: sudoriparous and sebaceous.

(1) The *sudoriparous*, or *sweat glands*, are exceedingly numerous. They are placed in the subcutaneous tissue, each being formed by a coiled tube lined by a single layer of columnar cells, presenting longitudinal striations. Starting from this coiled portion is a straight tube, which passes through the cutis vera, and, taking a spiral course through the cuticle, opens obliquely on the surface. The straight portion is lined by two or three layers of polyhedral cells. These rest on a basement membrane, and the lumen of the canal is lined by a bright homogeneous membrane, probably formed by the altered superficial portion of the epithelial cells. This is the only lining of the cuticular portion of the canal. In the coiled portion of the tube, a layer of unstriped muscle cells is found between the

basement membrane and the epithelial cells, placed longitudinally with regard to the long axis of the tube.

The *ceruminous* glands of the external auditory meatus are similar in structure to the sweat glands.

(2) The *sebaceous* glands are placed in the substance of the corium, while the ducts open into the hair-follicles, one or two into the neck of each. The duct divides into three or four branches, which end in saccular dilations, and are lined by polyhedral cells, the altered remains of which fill the lumen of the alveolus, forming the elements of the sebum. Between the lining cells fat globules are found, which fill the intra-cellular meshwork.

In a few situations very large sebaceous glands are found which open directly on the surface; these are found in the nostrils, scrotum, labia majora, &c. Tyson's glands, which are placed on the corona and prepuce of the male, and secrete the smegma preputii, also come under this head.

Hairs.—A hair consists of a *shaft*, which projects from the skin, and the *root*, which is imbedded in the hair-follicle. The root of the hair grows from a papilla at the bottom of the follicle, and this part presents an enlargement called the *bulb*.

The hair follicle and contained root are always placed obliquely with regard to the surface. The wall of the follicle presents an outer longitudinal and an inner transverse (or oblique) layer of fibre-bundles. The latter is often very indistinct, and reaches only to the openings of the sebaceous ducts. The longitudinal layer, which is stronger, is continuous with the papillary layer of the corium (Klein). On the inner side of the transverse is a layer of unstriped muscle cells, arranged horizontally to the surface. The lower part of the follicle presents a bulbous enlargement, the hair-papilla, and, at the bottom, these layers are thrown into its substance.

Within these layers is the *hyaline layer* of Kölliker, which reaches as high as the mouth of the follicle, where it is very thin; it is thicker as it passes downwards, and again grows thinner below, where it forms an extremely delicate membrane over the papilla. This layer is continuous with the basement membrane of the cuticle. Within it is the *outer root-sheath*, which is continuous with the epidermis, and presents all its layers (at least in the upper portion). This sheath is thickest in the middle of the follicle; in the lower part it is represented by

the rete Malpighii, and at the bottom it is reduced to a single layer of columnar cells which pass over the papilla.

Within the outer is the *inner root-sheath*, which is divided into layers; the outer is called Henle's layer, and the internal Huxley's. The former consists of small, clear cells, generally presenting no nucleus, while Huxley's layer consists of a single (sometimes a double) layer of oblong or cubical cells, each with an indistinct nucleus. Both these layers pass into the polyhedral cells of the superficial part of the papilla. The innermost layer of the inner root-sheath forms the *cuticle of the root-sheath*, and consists of flattened non-nucleated cells imbricated at their margin.

The shaft of the hair is made up of the *hair-cuticle, cortex, and medulla*. The cuticle consists of a layer of flattened scales, imbricated from the root towards the point. The cortical substance of the hair is made up of elongated, spindle-shaped, flattened scales, which may be separated by treating with strongly alkaline or acid solutions. Each is then found to contain a linear remnant of a nucleus (Klein). These scaly cells are arranged in groups, and between the groups are found rows of pigment granules in colored hairs, while in white hairs there are small air bubbles present. The medulla is absent in most hairs. When present it consists of one, two, or three rows of small polyhedral or cubical cells, each with a spherical nucleus (Klein). These cells contain minute air globules.

Connected with the hair-follicle is a bundle of unstriped muscle cells, the *arrector pili*, it ends, on one hand, at the surface of the corium, where the cells are arranged in plexiform bundles, and are lost in the connective tissue of the papillary layer; and, at the other extremity, it is continuous with a transverse zone of muscle cells, placed in the inner coat of the hair-sac, a little above the bulbous portion of the follicle. The direction of this muscular bundle is always oblique, and it forms a very acute angle with the axis of the hair, while it embraces, in a sling-like fashion, the base of the sebaceous gland.

Nails.—These are, like the hairs, cuticular appendages, formed by a modification of the rete Malpighii. A nail consists of: a *root* which lies on the *nail-matrix*, and is imbedded, at its posterior extremity, in a fold called the *nail-groove*; a *body* which lies on the *nail-bed*; and an *extremity* which projects free from the skin.

The substance of the nail is formed of transparent horny scales, each of which, when properly treated, presents the remnant of a flattened nucleus. The posterior part of the nail, called from its outline the *lunula*, is whitish in color, partly from the greater opacity, and partly from the diminished vascularity of that region of the matrix. The matrix presents elevations—leaf-like behind, and forming ridges in the distal portion, which bear papillæ on their convexities.

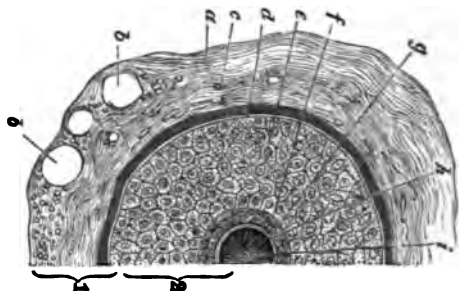


Fig. 63.

Cutaneous Secretion.—The secretion of the sudoriparous glands (*sweat*), is a colorless, transparent fluid of a saline taste and characteristic odor, which varies according to the different regions of the skin. The specific gravity is 1.001. The reaction is acid (according to most authorities), except in the axilla, where it is neutral or alkaline. But according to the recent researches of Luchsinger and Trümby, the normal reaction is alkaline, and the acidity is due merely to the fatty acids coming from the sebaceous matter which is mingled with the sweat, and by taking proper precautions to separate the secretions, as can be done in the palm of the hand, the reaction will be found alkaline. Sweat contains no histological elements, excepting epithelial scales which become mixed with it.

The quantity of the secretion is very variable (700—900 grammes per diem); but, under certain circumstances, it has been found to reach to over twenty times this quantity.

Chemical composition.—The sweat contains about ten parts of solid matters per 1000, of which one-half is formed by inorganic salts, among which the chief are the alkaline chlorides. The nitrogenous substances present are chiefly derived from urea,

which is present in the proportion of .44 per 1000 (Favre), or 1.55 (Funke). It contains, according to Leube, small traces of albumin. Traces of ammonia have been found, which probably came from the decomposition of the nitrogenous constituents. Favre has described a *hydrotic (sudoric) acid*, but its existence is denied by some other authorities. The non-nitrogenous constituents consist of volatile fatty acids (formic, acetic, butyric, caproic, propionic, &c.), which give the characteristic odor. The presence of lactic acid has been reported by some, and cholesterin and neutral fats, which come in part from the sebaceous glands. Coloring matters are also present, the composition of which has not been determined.

Special variations distinguish the secretion in certain parts of the body, especially the axillæ and soles of feet. When the quantity of sweat increases, the proportion of albumin, urea, and salts also increases, while that of the other principles diminishes. The *duration* of the secretion also influences the composition of sweat. The earlier portions are richer in fatty acids, the later in mineral salts. *Diet*, also, has its effect, animal food especially increasing its amount; drink, especially warm and alcoholic drinks, have a more marked effect. Everything that increases the activity of the cutaneous circulation has a similar action. An elevated temperature has this effect; a dry state of the atmosphere also favors the secretion, by promoting rapid evaporation.

Coloring matters of peculiar nature have been found in the sweat in some cases (*chromidrosis*).

The following table gives three analyses of sweat (per 1000 parts):—

	Favre.	Schottin.	Funke.
Water	995.573	977.40	988.40
Solids	4.427	22.60	11.60
Epithelium	—	4.20	2.49
Fat	.013	—	—
Lactates	.317	—	—
Sudorates	1.562	—	—
Extractives	.005	11.30	—
Urea	.044	—	1.55
Chloride of sodium	2.230	3.60	—
Chloride of potassium	.024	—	—
Phosphate of soda	traces	} 1.31	—
Alkaline phosphates	0.11		
Earthy phosphates	traces	.39	—
Salts in general	—	7.00	4.36

Many medicinal and other substances, when taken into the alimentary canal, find their way into the cutaneous secretion. Such are iodine, iodide of potassium, arsenic, alcohol, quinine, benzoic, tartaric, and succinic acids, &c.

Physiological functions of sweat.—This fluid may be regarded in the first instance as an excretory liquid, the separation of which is of a certain importance. In addition to this, however, we know that the sweat, by its evaporation, has a great influence on the regulation of the temperature of the body.

Secretion of Sweat.—The process of this secretion appears to be essentially one of filtration; epithelial desquamation, although more frequent in the sudoriparous glands than in the renal tubules, takes an unimportant part.

In addition to epithelial activity, the agencies which influence this secretion are the nervous system and the cutaneous circulation. Anything that increases the pressure in the cutaneous blood-vessels, promotes the secretion, and so does anything which increases the general blood-pressure. Many of the so-called diaphoretic medicines act in this way; some, on the other hand, seem to stimulate the glands directly, such as pilocarpin (jaborandi), muscarin, eserin, nicotin, morphia, &c. Atropin has the opposite effect. Prolonged heat or cold paralyses the sudoriparous glands (Luchsinger).

The innervation of the sweat glands has been carefully studied of recent years by Vulpian, Luchsinger, Nawrocki, Adamkiewicz, &c. As in other glands, two kinds of nerves may be distinguished, the *vascular (vaso-motor)*, and the *secretory* nerves properly so-called (*nerfs excito-sudoraux* of Vulpian). Usually the secretion is accompanied by vascular dilation, but this element is absent in some cases, as in the cold sweats produced by pain, and in certain febrile attacks. Sweating may be produced in an amputated limb in the absence of circulating blood, and Kitznadel has seen stimulation of the ulnar nerve produce, simultaneously, lowering of temperature and a profuse sudoriparous secretion. The nature of the influence of the vaso-motor nerves is still obscure; some refer the vascular dilation to paralysis of the vaso-constrictor nerves, while others explain it by stimulation of the vaso-dilator. Section of the sympathetic in the neck of the horse has been found by Dupuy to be followed by profuse sweating of the corresponding side of the face and neck; but galvanisation of the cervical sympathetic in man has been followed sometimes by sweating, sometimes by arrest of the secretion (M. Meyer, Nitzelnadel). The sudoral nerves of the posterior limbs of the cat have been shown to lie in the sciatic trunk; stimulation of the peripheral end causes an increase of the secretion; section of the nerve stops the secretion, but it reappears on stimulation by pilocarpin or by heat, even a week or more after the division. The sudoral fibres of the sciatic nerve come from the cord by the anterior roots, and partly from the abdominal sympathetic (Vulpian). For the anterior limb of the same animal they have a similar origin, and travel with the median and ulnar nerves. Those of the face, according to Luchsinger, come from the sympathetic, and join the branches of the trifacial. His results are opposed to those of Adamkiewicz, who found that stimulation of the facial nerve (beneath the skin) caused a secretion of sweat. The location of the *sudoriparous centres* has not yet been defined. Luchsinger admits the existence of spinal centres in the cat; for the anterior limbs, these are in the cervical part of the cord, while those for the posterior extremity are

placed in the part between the ninth and thirteenth dorsal vertebræ. Nawrocki has denied their existence, but Luchsinger attributes to the shock of the operation the negative results, obtained by that observer on section of the cord. Stimulation of the medulla oblongata of the cat has been followed by sweating of all four paws, even three quarters of an hour after death (Adamkiewicz).

These centres also present examples of *reflex action*. Stimulation of the central end of a divided spinal nerve causes an increase of the secretion. Irritation (electric, thermic, &c.) of the sensory nerves of the skin, is followed by local sweating; so is that of the mucous membranes, as in application of vinegar to the buccal mucous membrane. Psychical influences (fear, &c.) are followed by similar results.

The sudoriparous centres may also be directly stimulated, as by the condition of the blood in *asphyxia*; by *heated blood* at 45°C (113°F); also by the action of certain poisons (*pilocarpin*, *nicotin*, *eserin*).

Some of these poisons act *locally* on the sudoriparous glands. A hypodermic injection of pilocarpin is followed by a profuse secretion of sweat around the part; this secretion is arrested by an injection of atropin.

According to Vulpian, *inhibitory* sudoriparous nerves exist in the sympathetic. Hence, after section of the trunk, the secretion produced by pilocarpin is further increased; he also explains Dupuy's experiment in the same way.

When the sweat has passed into the cuticular segment of the gland-duct, it easily oozes into the intercellular spaces, as the duct in this part of its course has no proper wall. In ordinary conditions it there disappears by evaporation, constituting what is usually known as *insensible perspiration*. When the quantity of secretion surpasses the capacity of the epidermis for imbibition, the sweat appears in drops on the surface (*sensible perspiration*).

A peculiar hypothesis has been advocated by Krause and by Meissner, who believe that the sweat is eliminated from the papillæ of the cutis; they make the so-called sudoriparous glands the seat of a sebaceous secretion, only somewhat less dense than that of the ordinary sebaceous glands.

Sebaceous secretion.—This secretion is an oily, semi-fluid matter, which solidifies on exposure to the air. Microscopic examination shows fat cells, free fatty particles, with (sometimes) crystals of cholesterin, and epithelial scales.

The sebaceous secretion contains water, an albuminoid substance analogous to casein, fat (30 per cent.) consisting especially of palmitin and olein, soaps (alkaline palmitates and oleates), cholesterin, inorganic salts (especially the earthy phosphates, with some chlorides and alkaline phosphates).

Cerumen.—This substance which is secreted by the ceruminous glands of the external auditory canal, is an oily, yellowish substance, of very bitter taste. It is chiefly made up of fat globules, mingled with fat-cells and epithelial scales. Its composition in man is (per 1000 parts) as follows: water, 100;

fatty matter, 260 ; substances soluble in water, 140 ; substances soluble in alcohol, 380 ; insoluble matters, 120.

The sebaceous secretion lubricates the skin and hairs, and at the same time renders them impermeable to water.

Examination of the sebaceous glands has shown that the lining cells of the terminal portions of the duct become gradually infiltrated by fat, and when filled become detached from the basement membrane, and are gradually pushed towards the orifice by the young cells which grow up behind them. Before they are completely expelled, the nucleus and investing membrane will be found to have disappeared, and the fatty matter and epithelial debris which escape from the duct constitute the secretion.

LACHRYMAL SECRETION.

The *tears* are the secretion of the lachrymal gland. They form a colorless liquid, of salt taste, and alkaline reaction. They contain about 10 parts per 1000 of solids, which consist of mucus, and an albumin (*dacryolin*) which is precipitated by heat, with traces of fats and of mineral salts. The latter consist almost entirely of chloride of sodium, with a small proportion of the alkaline and earthy phosphates.

The following analysis is after Lerch :—

Water	.	.	.	.	982.0
Albumin and traces of mucus	.	.	.	.	5.0
Chloride of sodium	.	.	.	.	13.0
Other mineral salts	.	.	.	.	.2
					1000.2

The lachrymal glands are analogous in structure to the salivary glands, and their branching ducts end in similar acini, which are lined by glandular epithelium. The basement membrane is surrounded by a lymph-space, which separates it from a dense capillary plexus. The nerve-endings are not known.

The secretion is continuous, but very small in quantity, except under special circumstances. It takes place by filtration without any epithelial desquamation, or formation of mucus. The mucus present probably comes from the Meibomian glands.

It is powerfully influenced by the blood-pressure, hence anything that retards the venous circulation, such as laughing, coughing, vomiting, holding the breath, &c., increases the quantity.

In the ordinary conditions secretion is due to reflex stimulation, and the stimulus may be conveyed by the second

and third branches of the trigeminal nerve (from the conjunctiva nasal fossæ, &c.) or by the optic nerve (in irritation of the retina by a strong light). In the latter case, the secretion is bilateral ; in the former it is unilateral.

The principal secretory nerve of the gland is the lachrymal ; stimulation of the peripheral end causes an abundant flow of tears ; its section is followed, after a certain time, by a *paralytic secretion*. The nasal reflex persists after this section. It is not, however, the sole secretory nerve, the lachrymal branch of the temporo-malar, and the cervical sympathetic also influence the amount.

The lachrymal secretion is increased by calabar bean.

The tears when secreted pass along the ducts (10 or 12 in number) to the outer part of the retrotarsal fold, through which they pass into the superior palpebral sinus. From this they are diffused over the conjunctival surface, and the part which is not lost by evaporation passes into the lachrymal canal, from which they are conveyed along the nasal duct to the inferior nasal meatus. When the secretion is very abundant, they escape over the cheek.

THE MAMMARY GLAND AND ITS SECRETION.

The mammary gland is largely developed in the female, for the production of the nutritive fluid by which the young of mammalia are nourished during the early period of extra-uterine existence. A rapid increase of size marks the period of puberty in the human female. The central prominence (*nipple, mammilla*) marks the openings of the *galactophorous ducts*, of which about twenty are present. Each presents, a little beyond the base of the nipple, a dilation called the *ampulla*. The branches which come off from these main tubes divide and subdivide in the gland. Each terminal branch, after pursuing for some distance a more or less wavy course, terminates in a saccular dilatation called the *alveolus (acinus)*. This cul-de-sac is lined by a single layer of polyhedral or cubical cells, each with a spherical or slightly compressed nucleus. In some ducts a second layer of small round cells can be discovered beneath the others (Kolessnikow). The ducts are lined by a single layer of columnar cells, each of which contains an oval nucleus. They rest on a basement membrane, formed of a single layer of endothelial

cells (Langerhans). The larger ducts have strong fibrous coats with unstriped muscle cells between. They are derived from the cutaneous fibres, which abound in the skin covering the gland. At the nipple, the rete Malpighii of the epidermis is continued for some distance into the mouth of each duct (Klein).

Examination of the secreting gland has shown that the milk-globules collect in the lining cells of the alveoli, in a manner somewhat analogous to the accumulation of fat-globules in the cells of the connective tissue. During secretion, these globules are cast out into the lumen, and pass into the ducts as milk. Each milk-globule (?) possesses a delicate albuminous membrane (*membrane of Ascherson*). The first milk secreted after parturition (*colostrum*) contains large globules, which some regard as the epithelial cells which are cast off by the growth of new cells beneath. According to Rauber and Robin, however, the so-called *colostrum cells* are derived from leucocytes which had migrated into the alveoli, and undergone fatty degeneration.

The influence of *innervation* on the mammary secretion is not well understood. It is obviously present in the results of mental emotions on the secretion and composition of the milk, as well as in the relation of the gland to the genital organs, and the great increase produced by suction. The application of induced currents causes increased activity of the secretion, and may even bring it on in the inactive gland. Suction of the nipple has been known to cause the secretion to appear even in the mammary gland of the male, and a case of a male wet nurse (negro) is mentioned by Dunglison, with mammæ projecting 7 inches from the thoracic wall. Laffont, in his experiments on the bitch, found that stimulation of the peripheral end of the mammary nerve caused a copious secretion, and believes in the existence of *secretory* and *vaso-motor nerves* for the gland, but most other observers have failed to find results so definite.

Milk.—This secretion forms an opaque fluid, generally of a pure white color, with a characteristic odor, and sweet, saccharine taste. Its specific gravity is 1.028 — 1.034. Its reaction has been the subject of dispute; when fresh it is usually alkaline, but may be acid, and according to Soxhlet, its reaction is *amphicroitic*—it reddens blue litmus, and changes the reddened paper to its original blue. The acidity, when present, is due to the acid phosphate of soda and carbonic acid. Milk

contains fatty globules in suspension, which form a true emulsion, and give it its usual opacity.

Chemical composition.—Milk contains 110—130 parts of solid matter per 1,000. The following substances are present:—

(1) Nitrogenous substances, especially *casein* (4 per cent.), and a little *serum-albumin*;

(2) Fatty matters; which form the *cream* and butter, and are present as the *milk-globules* (2.5 per cent.);

(3) Milk-sugar (*lactose*, 4.5 per cent.); a ferment (*lactic ferment*);

(4) Traces of *extractives*, especially *urea*;

(5) *Mineral salts* in small quantity (2 per cent.); they consist of chlorides, phosphates, and alkaline carbonates, with sulphates of lime and of magnesia; traces of iron, of silicon, of metallic fluorides, and (perhaps) sulpho-cyanides are also present.

(6) Gases; especially CO_2 (7 per 100); with traces of N and O.

Other special *albuminoids* have been described: the *lacto-protein* of Millon and Commaille, which appears to be a mixture of casein and albumin; the *galactin* of Selmi is an impure form of albumin. The *milk-globules* are minute spherical bodies, of a diameter varying from $\frac{1}{1000}$ th to $\frac{1}{100}$ th of an inch. Most admit the existence of an albuminous investing membrane (*kaptogenous membrane* of Ascherson), and Schwalbe believes that he demonstrated its existence by staining with osmic acid, which blackens fatty matter. Sinéty has seen it plainly in the globules of colostrum, or of milk which had been allowed to stand for some time, after staining with rosaniline, which colors the coagulated proteids. This staining, however, failed to show it when the milk was quite fresh. According to Quincke, then, the fat is retained in a state of emulsion by the differences of tension produced at the surface of the fatty particles, which float in an albuminous liquid. Each droplet of fat becomes surrounded by a layer of casein, of which the pre-existence is due to causes purely physical.

The *lactic ferment* which causes the change of milk-sugar into lactic acid may be separated by dialysis, and treatment with alcohol and glycerine. The normal existence of *sulphates* in milk has been denied by some, but they have been repeatedly demonstrated in cow's milk by Ritter, Beaunis, and others.

Other substances have been found in milk: cholesterin, alcohol (Bechamp), butyric, lactic, and acetic acids; also odoriferous substances, soluble in sulphide of carbon (Millon and Commaille), &c. Many medicinal and other substances, when taken into the alimentary canal, pass into the mammary secretion: iodine, iodides, bromides, alkaline sulphates, salts of iron, of zinc, of mercury (this is denied by Kohler), of lead, of bismuth, of antimony, opium, indigo, the essences of anise, garlic, wormwood, &c.

Cow's milk is coagulated by all acids; acetic and tartaric acids redissolve

the coagulum. The coagulation takes place as soon as the quantity of acid passes the point of neutralisation of the casein. The milk of the human female is not coagulated by acids, it merely forms fine flocculi of a greyish-white color. The coagulation which milk undergoes in the stomach, is due (according to Hammarsten) to the action on the casein of a ferment, to which he has given the name of *lab*.

The following table gives the results of several analyses of the milk of the human female :—

In 100 parts.	Fr. Simon.	Becquerel and Vernois.	Joly and Fihol.	Tidy.
Water	883.6	889.08	874.6	878.1
Solids	116.4	110.92	124.8	121.9
Casein	34.3	39.24	9.8	35.1
Albumin	—	—	—	—
Butter	25.3	26.66	47.5	40.2
Milk-sugar ..	48.2	43.64	59.1	42.6
Mineral salts ..	2.3	1.38	1.1	2.8

It presents some variations in composition according to age, constitution, race, &c. A peculiar physiological fact is that the mammary gland of the newly-born foetus secretes a little milk (*lait des sorcieres*) for a few days after birth.

THE LIVER.

The structure of this gland, and the properties of its biliary secretion, have been studied in connection with the subject of digestion. In addition to this more obvious function of the liver as a secreting gland, there are others which it possesses as a vascular gland. Of these, the best known is its glycogenic function, in addition to which it appears to produce important modifications in the circulating blood, and probably aids in the formation of fats and of urea.

Glycogen.—The discovery of this substance, and the investigation of nearly all the laws which govern its formation and expenditure are owing to Claude Bernard. This substance exists in the liver in the normal state, and is converted into sugar by the action of a ferment. It may come from the food ingested, or be formed by the liver at the expense of some of the elements of the blood. It passes from the liver by the hepatic veins, and undergoes oxidation in the capillaries of certain organs.

Preparation of Glycogen.—Method of Cl. Bernard.—The liver of an animal is removed as rapidly as possible after death, cut into thin slices, and thrown into boiling water; the fragments are then bruised in a mortar and boiled for a quarter of an hour, with a little water. The fluid is then separated by pressure in a linen cloth; some animal charcoal is added, and it is filtered. An opalescent fluid is thus obtained, from which the glycogen is precipitated by adding four or five times its bulk of alcohol at 38° – 40° C. (100° .4– 104° F.) The precipitate is washed several times with alcohol. Boiling with a concentrated solution of caustic potash precipitates any traces of albuminoids that may be present, the excess of potash being afterwards removed by acetic acid. Ether removes the fat, by dissolving and carrying it to the surface.

Method of Brücke.—The fresh liver is plunged into boiling water; when hardened, it is pounded in a mortar, and then boiled in water for half an hour. A milky fluid is thus obtained, after the removal of which the liver-tissue is boiled with fresh water, and this is repeated till all opalescence disappears. The liquids are then mixed, cooled, and filtered. To the solution are then added alternately, hydrochloric acid and potassio-mercuric iodide, so long as a precipitate continues to form, and the fluid is again filtered. The filtered fluid is then treated with alcohol, which precipitates the glycogen, and the latter is washed several times with alcohol and purified by the ordinary methods.

Characters of Glycogen.—The glycogenic substance (*animal starch*, *hepatin* of Pavy, *zoamylin* of Rouget) is isomeric with starch and dextrin. The formula is $C_6H_{10}O_5$ or a multiple ($C_{30}H_{50}O_{25}$). It is a white, amorphous powder, having an insipid taste, and possessing no odor. It is soluble in boiling water, with which it forms an opalescent solution; insoluble in alcohol and in ether. The aqueous solution has a powerful dextro-rotatory influence on polarised light. The opalescence disappears on the addition of an alkali, with a solution of iodine in iodide of potassium. Glycogen gives a red coloration, which disappears on heating, but returns when the fluid cools. It does not reduce the test solutions of Fehling or Barreswill; it is precipitated by acetate of lead, which distinguishes it from dextrin; it is converted into dextrin and glucose by boiling with dilute acids, and undergoes the same modification when submitted to the action of diastatic ferments (animal or vegetable), or blood, saliva, &c. Animal charcoal removes all the glycogenic substance from its solutions.

The glycogenic substance is found during life in the hepatic cells of the liver, especially while digestion is going on. It exists there in the amorphous form, and not in the shape of granules, as Schiff believed. Its presence was first announced by Rouget in 1859, and, more recently, by C. Bock and A. F. Hoffmann. It is most abundant in the cells close to the sublobular veins.

The proportion of glycogen present in the liver varies in different animals; the average proportion is about 1.5–4 per 100 parts. The following table is from Dr. Robert M'Donnel,

ever, appear to believe that fat alone rather tends to diminish the quantity of hepatic glycogen.

With regard to the *nitrogenous* elements, most authorities agree with Cl. Bernard that their use increases the quantity of glycogen.

Beside the (larger) proportion derived from the food, it is believed by most authorities that the hepatic cells manufacture a certain quantity of glycogen independently of alimentation. During hibernation this substance accumulates in the liver, and Cl. Bernard has found that in birds, in which the operation succeeds best, ligature of the vena portæ does not prevent the formation of hepatic glycogen; but some think that this may be accounted for by the conveyance of the products of digestion, in a certain proportion, by the hepatic artery and its branches. The glycogen so produced is then probably formed at the expense of the blood, and not from the substance of the hepatic cells, as some have supposed, for in the liver which has been washed free of blood it ceases to appear; still it must be remembered that in such a case the change of glycogen into grape-sugar is so rapid, that it is very hard to determine whether the quantity of the latter corresponds to that of the glycogen, or if a part of the sugar is not due to the immediate transformation of some newly-formed glycogen.

An ingenious theory has been suggested by Heynsius and Kühne; it is that the glyccoll of the biliary acids is changed into urea and glucose:—



These observers have found that the ingestion of glyccoll increases, simultaneously, the glycogen of the liver, and the urea of the renal secretion.

According to Teflenbach, the hydrocarbons of food are not directly changed into glycogen, they merely act as special stimulants to the liver. Heidenhain inclines to a similar opinion, and mentions in its favor the fact that in diabetic patients the ingestion of saccharine food increases the quantity of sugar far beyond the proportion taken into the alimentary canal.

Other authorities (Weiss, Maydl, &c.) believe that the aliments have only an indirect influence on the formation of the hepatic glycogen; by their own affinity for oxygen the hydrocarbons prevent the oxidation of this substance, which, accordingly, is allowed to accumulate in the liver. This hypothesis (*theorie d'épargne*) leaves unexplained the origin of the glycogen.

After death it can be easily demonstrated, as was done by Cl. Bernard, that the glycogen is rapidly changed into glucose. If the liver be removed from the body of an animal immediately after death, and a current of cold water made to pass along the vena portæ, this water as it escapes from the hepatic veins is found to contain sugar, the quantity of which gradually diminishes to zero; at this moment the liver contains no glucose, but if allowed to stand for some time, a new quantity rapidly forms. This post-mortem formation of glucose is accelerated by moderate elevation of temperature; it is arrested completely by a temperature of 0°C. (32° F.), and by that of boiling. Dalton

found the following proportions of glucose at successive periods after death :—

After 5 seconds	.	.	.	.	1.8 per 1000.
— 15 minutes	.	.	.	.	6.8 —.
— 1 hour	.	.	.	.	10.3 —.

According to Cl. Bernard this change of glycogen into glucose is always going on during life. He has found by careful experiment, that in a dog fed on a purely animal diet, the blood of the portal vein contained no glucose, while that of the hepatic veins always yielded an appreciable quantity. This must, of course, come from the liver. Analysis of a portion of liver, taken from the body of a living animal, has also demonstrated the presence of sugar. These results have, however, been contradicted by Pavy, who failed to find sugar in the perfectly fresh liver, and believes its formation to be merely a post-mortem change.

The quantity of sugar in the liver increases in well-nourished animals ; it is also increased under the influence of æther, chloroform, morphia, by arrest (or other disturbance) of the hepatic circulation, or by ligation of the hepatic duct (Moos). It is diminished by fasting, by curara, and by ligation of the portal vein (this has, however, been denied by Cl. Bernard).

The change of glycogen into glucose is undoubtedly due to the presence of a ferment ; it may be separated by washing out the vessels completely, and then steeping the liver-tissue for two or three days in four or five times its weight of glycerine. The extract so obtained contains the ferment, which may be separated by precipitating with alcohol. It has been observed by Van Tielg that blood corpuscles at the moment of their destruction change glycogen into glucose in a temperature of 35° C. (95° F.).

Characters of Glucose.—This variety of sugar forms solid, white, inodorous masses, composed of rhombohedral tablets. It is soluble in water and in boiling alcohol, but slightly soluble in cold alcohol, insoluble in æther. It rotates the ray of polarised light to the right. It is changed by dilute nitric acid (when heated), into saccharic and oxalic acids. It is not blackened by concentrated sulphuric acid. Glucose forms with bases a series of soluble combinations (glucosates) analogous to salts. With beer yeast, especially at a temperature of 25° C. (77° F.) it undergoes the alcoholic fermentation :—



With cheese, sour milk, or albuminoids in a state of putrefaction, it undergoes, at first the lactic acid fermentation, then the butyric. It responds to several tests, of which the following are the most valuable :—

Reaction of Trommer.—On adding to a solution of glucose, a little caustic potash and solution of sulphate of copper, a light blue precipitate appears, which rapidly dissolves, forming an azure-blue color. On heating, an orange color appears, followed by the deposit of a yellowish precipitate of the hydrated sub-oxide of copper, or a red one of the anhydrous suboxide.

Reaction of Böttger.—(Under the same conditions) subnitrate of bismuth gives an olive-brown precipitate.

Reaction of Knapp.—The cyanide of mercury gives a dark precipitate.

Reaction of Sachsse.—A dark precipitate with mercurio-potassic iodide.

Reaction of Mulder.—On adding to a solution of glucose a solution of indigo made alkaline with carbonate of soda, the fluid at first becomes purple, and by boiling, yellow; on agitation it changes to blue, and when allowed to stand for some time, all the color disappears.

Reaction of Huisinga.—On heating a solution of glucose with some drops of the molybdate or tungstate of ammonia, and acidulating with hydrochloric acid, the liquid assumes a blue color.

In estimating the proportion of glucose present in the blood, this fluid is first boiled with sulphate of soda. The coagulated precipitate is removed by pressure and filtration, and the remaining fluid after addition of a certain proportion of potash and distilled water is cautiously dropped from a burette into the colored test solution.

According to the researches of Cl. Bernard, the liver is continually forming a certain proportion of glucose, which is carried off by the hepatic veins to be added to the general circulation. He was the first to demonstrate the presence of this substance in the blood independently of alimentation (1849). The presence of sugar in the blood of diabetic patients had been shown by MacGregor (1837), and it was found (in the same year) by Bouchardat, after ingestion of large quantities of saccharine food.

A distinction must then be made between the two conditions; in one of which the glucose is formed by the liver independently of alimentation, while, in the other, a supply of material for the manufacture is afforded by the ingestion of various hydrocarbons. In the former case, no trace of glucose can be detected in the blood of the vena portæ; that of the hepatic veins contains an appreciable quantity. This can also be found in the inferior vena cava, right side of heart, and pulmonary arteries. The arterial blood is found to contain a similar quantity, but the venous blood returning from the systemic *capillaries* yields a much smaller proportion.

When the contents of the alimentary canal furnish glucose, the substance so absorbed is found in variable quantity in the vena portæ, and may exceed in proportion that of the hepatic veins. The proportion of sugar in the other segments of the vascular system does not, however, vary from that in the preceding case. So that the quantity of sugar in the vena portæ is variable; while it remains constant in the hepatic vein, and throughout the rest of the vascular system it is also constant, and independent of alimentation. This normal proportion in man is .9 per 1000, according to Cl. Bernard. The ratio is increased by bleeding; inanition at first increases, and afterwards lessens the quantity.

It is increased in asphyxia (Dastre). When it passes certain limits (4—6 per 1000) glycosuria results. After ligation of the vena portæ, ingestion of a small quantity of sugar produces glycosuria, and a similar result occurs in cases of hepatic cirrhosis.

The results of Bernard have, however, met with a good deal of contradiction, especially from Pavy and V. Mering. Bock and Hoffmann have found the sugar of the blood disappear after ligation of the thoracic duct.

Role of the hepatic glycogen.—According to the observations of Bernard as above related, the destruction of the sugar of the circulating blood takes place in the course of the systemic capillaries, and there alone. It was at one time believed by some observers that the glucose was largely oxidised in the passage of the blood through the pulmonary capillaries, but this notion has been disproved by comparative analyses of the blood of both sides of the heart. The later researches (by Cl. Bernard, Tieffenbach, Weiss, &c.) go to prove that the oxidation of glucose takes place chiefly in the muscles; that, in fact, the hepatic glycogen is the great combustible material which is used up by the muscles during their contraction. If the muscles of a limb be tetanised by stimulation of the nerve-trunk, the sugar is destroyed more rapidly in the blood. Glycogen is now known to be a constituent of living muscle, and it has been found by Weiss that if the muscles of one limb of a frog be tetanised, they will contain less glycogen than those of the resting limb. This would afford an explanation of the artificial glycosuria which is produced by curara poisoning.

Influence of the nervous system.—The first discovery in this direction was by the celebrated experiment of Cl. Bernard, who found that puncture of the floor of the fourth ventricle at the level of origin of the pneumogastric nerves was followed in the rabbit by glycosuria of 5—6 hours, and, in the dog, by a similar result lasting for a somewhat longer time. If the hepatic glycogen has been used up by inanition, glycosuria will not follow (Dock). That the sugar comes from the liver is shown by the fact that if the vessels of that organ have been previously tied, none appears in the urine after the "diabetic puncture"; also that glycosuria does not occur in the frog during winter, while the liver contains no sugar (Schiff). Besides an increase of the sugar of the blood, a portion appears in the bile after the diabetic puncture, and this secretion is slower after the operation (Jeanne-ret). Previous ligation of the biliary ducts has been found to prevent the occurrence of glycosuria in the cat (Wickham Legg). Previous ingestion of glycerine prevents, according to Luchsinger, the usual result of the diabetic puncture, but this assertion has been contradicted by Eckhard.

Stimulation of the central end of the pneumogastric, of the depressor nerve (Filehne, Laffont), section of the annulus of Vieussens, removal of the last cervical or first dorsal ganglion of the sympathetic (Cyon and Aladoff), section of the superior cervical ganglion (Pavy), extirpation of the coeliac (semilunar) ganglion (Munk), form a series of experimental modes of production of artificial diabetes. The same result follows division of the spinal accessory nerve (Schiff), division of the plexus of nerves which accompanies the vertebral artery in the foramina of the transverse processes of the cervical vertebræ (Pavy), section of the splanchnics (sometimes), stimulation of the second lobule of the median lobe of the cerebellum (Eckhard), or stimulation of the upper part of the spinal cord.

If the splanchnic nerves have been previously divided, glycosuria does not follow the diabetic puncture; but if the nerve section be subsequent to the puncture, it does not interrupt the usual sequence of events.

The explanation of the result of the diabetic puncture given by Cl. Bernard is that it acts as a stimulant to a number of vaso-dilator nerves, which have their origin in the medulla oblongata, and ultimate distribution in the liver. The early disappearance of the glycosuria may be due to the hæmorrhage which supervenes upon the puncture, and paralyses the vaso-dilator centres (Laffont). These nerves travel with the cord for a little, and afterwards join the sympathetic. A portion of the fibres, at least, accompany the vertebral plexus, and pass from the last cervical ganglion to the first dorsal, along the annulus of Vieussens. From the thoracic sympathetic they travel with the splanchnic nerves to the solar plexus, and thence to the liver. A portion accompanies the spinal cord to the upper dorsal region, and passes to the sympathetic along the communicating branches of the two or three upper dorsal pairs of nerves. Accordingly, section of these nerve fibres in any part of their course will be followed by the same result as puncture of the floor of the fourth ventricle itself. The glycosuria produced by stimulation of the other nerves mentioned, is explained by reflex stimulation of the vaso-dilator nerves. With regard to the influence of the nervous system on the formation of glycogen in the liver, Cl. Bernard found that section of the cord between the last cervical and first dorsal vertebræ caused an accumulation of glycogen, while sugar disappeared completely from the blood and from the liver. In rabbits kept long fasting, for the purpose of causing disappearance of the hepatic glycogen, the following results have been obtained by J. Meyer: (1) section of the cord between the fifth and sixth cervical vertebræ prevents the formation of this substance in the liver; (2) section between the last cervical and first dorsal vertebræ increases the production; section between the second and third dorsal vertebræ diminishes it.

Embryonic glycogen.—Claude Bernard soon after his discovery of the hepatic glycogen, found that the same substance existed during foetal life in many of the tissues of the embryo: muscles, lungs, epithelium of skin and mucous membranes, and in the placenta; the proportion present in these tissues was also found to diminish as the development of the liver progressed, till, at birth, little remained except in the muscles.

In addition to the nervous influences productive of diabetes, there are a number of substances which cause this result when absorbed: such as

chloroform, ether, chloral, sulphide of carbon, nitrite of amyl, curara, carbonic oxide, morphia, &c.

The amount of light which has been thrown on the subject of physiological diabetes, has not proved sufficient to explain the occurrence of the permanent glycosuria which is met with in disease. The following table, enumerating the various hypotheses which have been advanced on the subject, is taken from Beaunis :

A. Where the cause exists in the liver.—(1) The activity of the liver is diminished, and the glucose coming from the alimentary canal is not changed into glycogen (Zimmer, Tscherinow). (2) The glycogen passes into the blood and is then changed into sugar (Pavy). (3) The production of sugar in the liver is augmented by increased activity of the liver, by prolonged contact of the ferment with the hepatic cells, or exaggerated production of the ferment. (4) The hepatic circulation is accelerated, and the hepatic cells have not time to convert into glycogen all the sugar carried up by the portal vein (Luchsinger). (5) Diabetes is due to peripheral stimulation of the branches of the pneumogastric in the liver (Harley).

B. The diabetes is due to incomplete oxidation of the sugar.—(1) Diminution of the respiratory capacity of the red globules (Voit, Bock, Hoffman).

(2) A general trouble of assimilation (Rosenstein, Schultze). (3) Respiratory trouble (Reynoso). (4) Muscular inactivity (Winogradoff). (5) Diminished alkalinity of the blood (Miahle).

C. That diabetes is due to a disturbance of nutrition.—(1) The organs have lost their power of assimilating sugar (Seelig). (2) The dissimilation of the tissues is exaggerated, especially of their glycogenic substance (Sansou, Rouget).

D. The digestion of saccharine food in the intestine takes place too rapidly (Bouchardat).

E. Diabetes is due to a nervous influence, of which the centre is placed in the medulla oblongata and origins of the pneumogastric nerves.

F. Diabetes is produced by an affection of the pancreas (Pipper).

Production of fat in the liver.—The hepatic cells have a marked tendency to the accumulation of fat, especially in the circumferential zone of the lobules (corresponding to the branches of the vena portæ). This is more marked in pathological conditions. The accumulation is intimately connected with the glycogenic function of the organ ; indeed, according to Tscherinoff, the hepatic glycogen is partly converted into glucose, and partly into fat. This fat is very easily oxidised (as is seen in that of the cod's liver), and, in this way, it diminishes the quantities of oxygen required for respiratory purposes. Accordingly, a kind of balance is kept up between the lung and liver, and several physiological facts show the existence of this vicarious action. Where the respiration is very active, the liver is always small, as in birds ; where, on the other hand, the respiratory process is slow, as is seen in the embryo and in fishes,

the liver is of voluminous dimensions (Neumann). During the time of lactation, the liver contains much fat ; but, contrary to what occurs in the ordinary fatty liver, it is deposited in the central part of the lobule (Sinéty).

Influence of the liver on the blood (*hæmatopoietic function*).—Two different actions on the corpuscles have been attributed to this organ ; according to some it is a generator, according to others, a destroyer, of blood corpuscles ; while some believe that it simultaneously exercises both functions.

It is very probable that the liver destroys a portion of the red blood corpuscles. Bilirubin seems to be a direct derivative from hæmoglobin, the latter losing its iron ; and, Naunyn has found that on injecting a solution of hæmoglobin into the vena portæ, this substance was changed into bilirubin. The biliary acids are known to have the power of decomposing hæmoglobin, and are, probably, the active agents in this case.

In comparing the characters of the blood of the portal and hepatic veins, Lehmann found the corpuscles in the latter smaller, more spherical, and having less power of resisting water ; in short, that they appeared to be of more recent formation. He, accordingly, advanced the hypothesis that these young cells were formed in the liver, but the evidence on the subject is not precise enough to warrant our drawing any definite conclusions on the subject.

Formation of urea in the liver.—This hypothesis had been enunciated by Heynsius and Kütke, and more recently advocated, with great ability, by Meissner, who especially calls attention to the fact, that urea disappears from the urine in cases of acute atrophy of this organ. The liver always contains a considerable quantity of urea, and, as Cyon has shown, if a current of blood be passed through the vessels of this organ, it is found, after escaping, to contain an appreciable amount of urea. This urea is formed at the expense of the red blood corpuscles (Meissner, Huppert, Beneke). Other experiments, however, tend to overthrow this hypothesis. J. Munk, in four experiments, found less urea in the liver than in the blood, and Gschleiden found no more urea in the hepatic than in the portal vein, nor did he find any accumulation of this substance when the liver was left to itself after removal from the body. Picard, however, has, on the last point, arrived at a contrary conclusion, and Stolnikow has found, in recent experiments,

that electrification of the liver, in man and in the dog, was followed by an increase in the urea of the renal secretion. He has also found that by electrification of a mixture of pounded fresh liver and defibrinated blood, a large formation of urea resulted.

Relation of the biliary secretion and the glycogenic function.—By some authorities (Morel, Handfield Jones, Henle, &c.) it has been attempted to separate the regions of the hepatic organ allotted to these functions. The liver, according to these physiologists, may be considered as formed by two glands: one, a vascular glycogenetic structure formed by the hepatic cells and the portal vein; the other, a biliary gland, formed by the biliary ducts with their attached mucous glands, and the hepatic artery. An argument in favor of this hypothesis, brought forward by Küss and Duval, is the continuation of the biliary secretion in cirrhosis and in fatty liver, notwithstanding the altered condition of the hepatic cells. These arguments are, however, inconclusive, and the intimate relation of the bile capillaries to the hepatic cells seems to forbid us to separate the two great functions of these structures. Beaunis supposes that the water and soluble salts of the bile are separated by filtration in the small racemose glands which are attached to the bile ducts, while the other constituents of this secretion are formed in the hepatic cells.

Antitoxic action of the liver.—Schiff and Lautenbach have arrived at the conclusion that the liver has a distinct power of destroying certain organic poisons. A dose of nicotin, which would cause certain death if introduced into the sub-cutaneous tissue, does not at all endanger life if introduced into the intestine, or injected into one of the branches of the vena portæ. Trituration with a fragment of fresh liver has also been found to diminish greatly the toxic powers of this poison, and the antitoxic power of the liver has also been found to exist for hyoscyamin to a still greater degree. It has also been found with conicin, and with the venom of the cobra (Lautenbach). Schiff believes, that in the normal state there is a very energetic poison produced in the animal organism, which is destroyed in the liver. After ligation of the vena portæ or extirpation of the liver, this substance accumulates in the system. The hypothesis has not, however, received any verification.

Chemistry of the liver.—The reaction of the fresh liver is alkaline; it becomes acid after death. When freed from blood by injection of a weak saline solution, the hepatic cells are found to contain the following substances: albuminoids (albumin, myosin), nuclein, nitrogenous extractive matters (xanthin, hypoxanthin, uric acid, urea), lactic acid, glycogea,

glucose, an hepatic ferment, fat, coloring matter, mineral substances (especially the phosphates of potash and soda, and the phosphate of iron).

The following analyses of hepatic tissue are by V. Bibra:—

1,000 parts.	Man.	Ox.	Calf.
Water	761.7	713.9	728.0
Solids	238.3	286.1	272.0
Insoluble tissues	94.4	121.3	110.4
Soluble albumin	24.0	16.9	19.0
Glutin	33.7	65.1	47.2
Extraction matter	60.7	53.1	71.5
Fat	25.0	29.6	23.9

THE KIDNEY AND URINE.

The kidney, or gland which fulfils the important function of secreting the urine, is a compound tubular gland, of a well-known characteristic shape, and weighing about 5 ounces. The depression on its inner border which contains the vessels and duct (*urder*) is called the *hilum*. The ureter, where it is connected with the hilum presents a dilatation called the *pelvis*, and is lodged in the depression at the posterior part which is called the *sinus*. If a section be made of the kidney from the convex to the concave edge, its substance is seen to be made up of two distinct parts, the *cortical* and the *medullary*. The cortical substance occupies the superficial part of the organ for a depth of about a quarter of an inch, and presents to the naked eye a rather uniform vascular structure. The *medullary* portion, on the other hand, presents two distinct parts. A number (8-18) of cones (*pyramids of Malpighi*) are placed with their apices towards the hilum, while the substance between, which looks like a continuation of the cortical substance, forms the so-called *columns of Bertin*.

The *pelvis* of the kidney divides in the *sinus* into three *infundibula*, which in turn, subdivide into *calyces*. The *calyces* embrace the *papilla*, which are formed by the apices of the pyramids, each apex forming as a rule a single papilla; but, in a few instances, two or more apices join to form one papilla. Each calyx also receives a single papilla, but in each kidney we find one or more exceptions, two or even three papillæ being embraced by a single calyx.

The lining membrane of the *pelvis*, *calyces*, and *infundibula*,

is continuous with that of the ureters, and, like the latter, is lined with stratified transitional epithelium, while beneath the submucous tissue are muscle cells, arranged as an external longitudinal and an internal circular layer. On the papillæ, circular fibres alone are found (Henle).

In the cortical substance are placed the *Malpighian corpuscles*, which, with the *uriniferous tubes*, form the physiologically essential part of the organ. The diameter of a Malpighian body is about $\frac{1}{16}$ th of an inch, and it contains a capillary plexus (*glomerulus*) enveloped by a homogeneous membrane, which is lined by a single layer of flattened cells. This layer is reflected over the capillary plexus. Coming off on one side of the capsule is the uriniferous tube, and at the opposite side of the circumference it is pierced by the afferent artery (*vas afferens*), and the efferent vein (*vas efferens*).

Leaving the Malpighian corpuscle, with the capsule of which its coat is directly continuous, the uriniferous tube begins by a constriction (*the neck*) below which it immediately expands to form the *proximal convoluted tubule*. This after several turns passes into the *spiral tube of Schachowa*, which takes a more regularly downward direction, towards the Malpighian pyramid. Passing from the cortex into Ludwig's boundary layer, the tube becomes suddenly very narrow and straight, forming the *descending limb of Henle's loop*. This passes into the pyramid for a variable distance, and turning forms the *loop* itself, from which it passes into the boundary layer again, forming the *ascending limb of Henle's loop*, which is also of considerable width. It then becomes narrower, and forms another definite segment as the *spiral tube of the ascending limb*. From the upper end of this part it continues to ascend, in somewhat narrower form, and, usually, slightly wavy course, and, after a variable distance, passes into the cortex, where it forms the *irregular tubule*, which is very irregular in width and direction. This segment is then continued into the *distal convoluted tubule*, or *intercalated segment* (*Schalstück*) of Schweigger-Seidel, which joins the curved part of the collecting tube. A number of the latter having joined, the collecting tube becomes straight, and, passing through the boundary layer into the papilla, it forms one of the large collecting tubes (*straight tubes of Bellini*), which, by joining other ducts increases in size, as it passes towards its termination on the apex of the papilla.

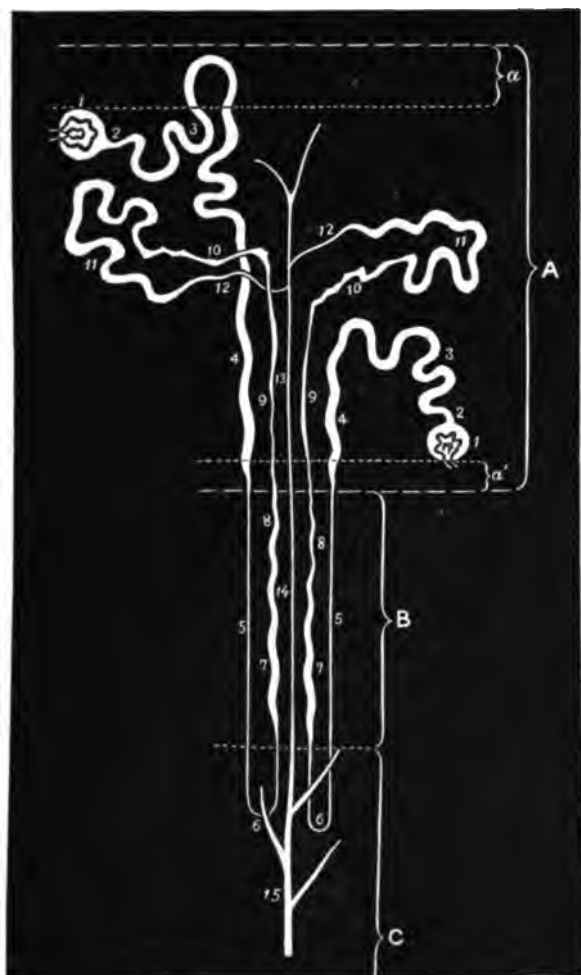


Fig. 64. A diagram of the sections of uriniferous tubes. A, cortex limited externally by the capsule; a, subcapsular layer not containing Malpighian corpuscles; a', inner stratum of cortex, also without Malpighian

capsules ; B, boundary layer ; C, Papillary part next the boundary layer : 1, Bowman's capsule of Malpighian corpuscle ; 2, neck of capsule ; 3, proximal convoluted tube ; 4, spiral tubule of Schachowa ; 5, descending limb of Henle's loop ; 6, the loop proper ; 7, thick part of the ascending limb ; 8, spiral part of ascending limb ; 9, narrow ascending limb in the medullary ray ; 10, the irregular tubule ; 11, the intercalated section of Schweigger-Seidel, or the distal convoluted tubule ; 12, the curved collecting tubule ; 13, the straight collecting tubule of the medullary ray ; 14, the collecting tube of the boundary layer ; 15, the large collecting tube of the papillary part which, joining with similar tubes, forms the duct. (Klein and Noble Smith.)

The *epithelium* varies in the different sections of the tubuli uriniferi. In the neck the epithelial lining seems absent, "the membrana propria alone forming the wall of this part" (Klein). The membrana propria presents in some places oblong flattened nuclei, as if it were composed of endothelial plates (Klein). The epithelial cells of the descending limb of Henle's loop, and of the loop itself are very flat and transparent, while those of the collecting tubes are columnar in form. In all the other segments the epithelial cells are distinguished by their striations or *rods*, placed vertically to the surface of the basement membrane. These are best marked next the basement membrane, and are regarded by Klein as septa of a honey-combed network seen in profile. They are most distinct in the irregular portion of the tube.

Blood-vessels. The vascular supply of the kidney presents very marked peculiarities. The branches of the renal artery ascend in the columns of Bertin to the boundary layer, and there give off short trunks which divide into a number of *vasa recta* (*arteriole recta*). These pass down between the bundles of uriniferous tubes, and, towards the apex of the papilla, break up into a capillary plexus for the supply of the tubes. The ascending branches which pass into the cortex are called *interlobular* ; from these the *vasa afferentia* pass to the Malpighian corpuscles. On entering the capsule the afferent artery, as already mentioned, breaks up to form a capillary plexus, and at the centre of this plexus begins the efferent vein, which is *smaller* than the artery. Emerging close beside the latter, the *vas efferens* soon breaks up into a dense plexus of capillaries, which surrounds the tubes, both of the cortex, and of the adjacent part of the boundary layer, and making, in the former situation, dense polygonal meshes ; in the latter, a more open network. Venous *vasa recta*

accompany the arterial, and all converge, at the junction of the cortex and medulla, to the large venous trunks which join to form the renal vein. The capillaries of the subcapsular layer of the cortex converge from the surrounding parts, to form minute venous rootlets, giving rise to a stellar arrangement (*stellula Verheyenii*). The efferent vessels of the Malpighian bodies are looked upon by some authorities (Cleland, &c.) as truly arterial. The peculiarity of their arrangement, commencing and ending in capillaries, suggested to Bowman a comparison with the vena portæ (portal system of the kidney).

To the structures above described is relegated the important function of the secretion of urine. To explain the mechanism of the secretion, which even still remains an unsettled question, three principal theories have been advanced:

(a) *Bowman's*.—The watery part of the urine, and, perhaps, the more soluble salts, are separated in the glomerulus; the solids are secreted by the epithelium of the tubules, and swept down by the water in its descent. The more recent experiments of Heidenhain confirm the opinion of Bowman. After division of the upper part of the spinal cord, for the purpose of arresting the flow of urine, he injected indigo-carmin into a vein. By repeating the experiment a sufficient number of times, and removing the kidneys at measured intervals, he was able to trace this substance through the epithelial cells, and so into the tubules, in the interior of which it remained, as there was no urinary flow to carry it off. No trace of the pigment could, in any case, be detected in the glomeruli. The portions of the tubules whose cells took up the pigment, were those in which the epithelium presents the rod-like striations above mentioned. If urea be injected into the blood-vessels it gives rise to a copious secretion of urine which washes it away before any conclusive observations can be made; but in the amphibia, where the kidney receives a double vascular supply, positive evidence of the excretion of urea is afforded by experiment. In these animals the renal artery entirely supplies the glomerulus, while the renal vena portæ (from the anterior abdominal vein) forms the plexus which surrounds the uriniferous tubules. If the renal artery be tied, it has been found by Nussbaum, that sugar or peptones do not appear in the urine after being injected into the blood, although they readily pass through the intact organ. But urea, when introduced into the circulation, causes a flow of urine

even after deligation of the renal artery. If indigo-carmin be injected the pigment can be traced, as in the experiment already mentioned, into the tubules, but its passage is not accompanied by a secretion of urine. These experiments clearly demonstrate the elimination of the urea and less soluble materials by the epithelial cells. Why it is, that urea causes a copious secretion of the watery constituents of urine, under all circumstances, cannot be explained.

(2) *Ludwig's*.—According to this hypothesis the blood-pressure is the sole efficient factor in the elimination of urine. The intra-glomerular pressure is normally high because the vas efferens is of smaller size than the afferent vessel, and breaks up into capillaries again a short distance from the Malpighian body.

Under the influence of this pressure, the plasma, minus the albuminoids and salts, filters through the capillary walls within the glomerulus, and, passing along the tubules, undergoes an appropriate concentration, by osmotic exchange with the contents of the peritubular lymph-spaces. The limited power of diffusion of the albuminoids and fats with acid fluids accounts, according to Ludwig, for their not passing into the tubules with the other constituents of the plasma, in presence of the free acid of the urine which is always formed in the kidney. The very great difference in proportion of the solids of the urine, and of those of the blood, makes another difficulty in this theory of which it is less easy to offer a plausible explanation.

(3) *Küss's*.—The blood plasma passes through the capillary walls, as in an ordinary serous transudation. In its descent along the tubules it loses the albumin which is taken up by the epithelial cells, while re-absorption is favored by the low pressure of the blood in the peritubular capillaries. This theory explains the fact that the cysts which form after obliteration of the uriniferous tubes are found to contain not urine, but a serous fluid containing albumin; also, the appearance of albumin in the urine in morbus Brightii, when the epithelial cells have disappeared, or undergone degeneration. How the absorption of the albumin by the epithelial cells takes place remains unexplained.

A comparative examination of these different theories shows that each presents heavy objections to its acceptance. That the *blood-pressure* exercises a very powerful influence on the urinary

secretion cannot be denied, as the quantity is found to vary with every known cause which affects this condition. The influence of the *condition of the blood* is also of very great importance, as every diffusible material introduced into the circulation, is found to appear in the urine with great rapidity. The nature of the *activity of the glandular epithelium* still remains unexplained. The microscopic appearances of the cells, and the results of the above-mentioned experiments, are in favor of their secretory function; while the length of the uriniferous tubes, and the complex tortuosity of their course, seem to point to an absorbent action.

The following comparative analyses will be of interest in connection with the questions which we have just been discussing :

In 1000 parts	Urine	Blood-plasma	Lymph-serum
Water . . .	960.00	901.51	957.61
Albuminoids . . .	—	81.92	32.02
Fibrin . . .	—	8.06	—
Urea . . .	23.30	.15	—
Uric acid . . .	.50	—	—
Chloride of sodium . . .	11.00	5.546	5.65
Phosphoric acid . . .	2.30	.192	.02
Sulphuric acid . . .	1.30	.129	.08
Earthy phosphates . . .	.80	.516	.20

Urine—The urine of man in the normal state is a limpid fluid, with a slight straw or amber tint, possessing a characteristic aromatic odor, and a saline (somewhat bitter) taste. Its specific gravity ranges between 1.005 and 1.030, averaging about 1.020. Its reaction is usually acid. The daily quantity (which is very variable) averages about 1000—1400 cubic centimetres. It contains no anatomical elements, excepting (occasionally) a few epithelial cells detached from the urinary passages.

The *color* of urine varies with its degree of concentration, quantity, alimentation, &c. That passed in the morning (*urina sanguinis*) has the deepest tint; that passed after meals (*urina cibi*) is a little less so tinged; after drink (*urina potus*) it is nearly colorless. The urine of females is paler than the secretion of males, and that of the newly-born foetus is entirely colorless after the first emission. In infancy, it is of a pale yellow tint. The color of normal urine is due to the presence of *urobilin* or its chromogen, and some other coloring matters, the nature of which is not fully known. In disease the urine often undergoes

very pronounced changes in color, and many coloring matters (animal and vegetable) when taken into the alimentary canal pass into this secretion (bile, senna, rhubarb, santonin, &c.) The transparency is sometimes diminished by epithelial debris, fat (as in chylous urine), urates, oxalates, mucus, &c. &c. The spectrum of urine in many cases shows, after addition of an acid (and sometimes without any preparation), the bands characteristic of urobilin.

The *specific gravity* of urine varies according to the relative proportion of solids present, and is generally in inverse ratio to the quantity. It has been tried to estimate the proportion of urinary solids by multiplying the two last figures of the density by 2 (Trapp), by 2.2 (Loebisch), by 2.33 (Haeser), and by 2.3092 (E. Ritter) ; but such a proceeding can give, at best, but unreliable results.

The *reaction* of urine is due to the presence of acid phosphate of sodium, and does not appear to depend on the presence of a free acid, for it gives no precipitate with the hyposulphite of sodium. It sometimes gives an *amphicrotic reaction*, turning blue litmus paper red, and red litmus paper blue ; this peculiarity has not been explained.

The acidity increases by fasting, by muscular exercise, and by ingestion of acids ; it diminishes, and may even be replaced by alkalinity, during digestion (on account of the quantity of acid eliminated with the gastric juice ?), after ingestion of alkaline carbonates, of salts of the vegetable acids, of phenol, by warm baths, &c. Admixture of the vaginal secretions sometimes gives an alkaline reaction to the urine of females ; that of the newly-born foetus is neutral or very feebly acid. The acidity of the urine of 24 hours corresponds to that of 2 to 4 grammes of oxalic acid.

The *quantity* of urine varies with many conditions. During the first day of extra-uterine existence it measures but a few cubic centimetres ; at the end of the first month it reaches to 200 or 300 cc. ; between the ages of 3 and 5 years it reaches a mean of 750 cc. for boys, 800 for girls. The secretion increases after meals (especially when much fluid is taken) ; it diminishes during sleep. It also varies with the quantity of water eliminated by the skin and lungs. It diminishes when sweating takes place, and when the blood-pressure is lowered from any cause ; it increases with the increase of renal blood pressure, and after

ingestion of many substances passing easily into the secretion, such as urea, sugar, &c. A number of other substances (so-called *diuretics*) have a similar effect, but the *modus operandi* of some is not clearly understood.

Chemical Reactions of Urine.—The addition of hydrochloric acid gives a dark tinge to the urine, which develops a characteristic odor, and, at the end of 24—48 hours deposits crystals of uric acid. If to hydrochloric acid one-third of the bulk of urine be added, the latter gives a marked change of color (cherry-red, reddish-brown, violet, or blue). On the addition of nitric acid, there forms at the junction of the two liquids a zone of garnet-red hue (*urophæzin* of Heller), and on mixing the two liquids the urine appears of a darker color. It is also darkened by sulphuric acid. Picric acid precipitates crystals of uric acid. Acidulated by nitric acid, then treated by phospho-molybdic acid and boiled, it presents an indigo-blue coloration. Alkalies give a whitish precipitate of the alkaline earthy phosphates, Urine decolorises the iodide of starch; it is made turbid by addition of chloride of sodium; it gives precipitates with nitrate of silver, acetate of lead, and oxalate of ammonia. A dilute solution of nitrate of mercury causes turbidity, which disappears by agitation; heated with an ammoniacal solution of oxide of copper it is decolorised.

Chemical Composition of Urine.—The urine of 24 hours contains about 60 grammes of solid matters, of which about 40 grammes are organic matters, while 20 are formed by the inorganic constituents. The following substances are included:

(1) *Nitrogenous compounds*, which come from the metamorphosis of albuminoids, or of their derivatives: urea, uric acid, creatinin, hippuric acid, traces of xanthin, oxaluric acid, and (sometimes) allantoin;

(2) *Non-nitrogenous compounds* (these exist in smaller quantity); oxalic acid, lactic acid, glucose; sometimes traces of volatile fatty acids, of succinic acid;

(3) *Sulpho-conjugate acids*; indican, pheno-sulphuric and creso-sulphuric acids, sulpho-pyrocatechic acid;

(4) *Coloring matters*; urobilin or its chromogen, and probably other pigments still imperfectly known;

(5) *Inorganic substances*; chloride of sodium and of potassium; acid phosphates of sodium, of lime, and of magnesia; alkaline sulphates; traces of ammonia and of iron;

(6) *Gases*; especially carbonic acid, nitrogen, and a small proportion of oxygen.

In addition to the normal constituents above named, some other substances are exceptionally present, or are at least of doubtful constancy. Such are: traces of albumin, of peptones, a saccharifying ferment (*nephrosymase* of Bechamp), sulphocyanide of potassium, a volatile fatty acid which has not yet been isolated (Schönbein), a substance which has a lævo-rotatory action on the plane of polarised light (Haas), biliary acids (Dragendorff, Naunyn), cryptophanic acid (Thudichum), the lactic diamide of Baumstark, protoxide of hydrogen (Schönbein), silicic and nitric acids derived from the fluids taken into the alimentary canal, &c. In some cases there are also found: mucin, inosit, hypoxanthin, leucin, tyrosin, cystin, fats, sugar of milk (during lactation), formic acid, alcohol, acetone, hyposulphite of sodium, &c. After the ingestion of vegetable acids, the urine is always found to contain alkaline carbonates. In pathological conditions it may contain blood (hæmaturia), albumin (albuminuria), the coloring matters and the acids of bile (icterus), glucose (diabetes), &c.

After being allowed to stand for some time urine becomes somewhat darker in color; this change is probably due to absorption of oxygen, and oxidation of the urinary pigment (Pasteur). It acquires a greater acidity (*acid urinary fermentation*), while a whitish pellicle forms on the surface, and crystals of uric acid, urates, and oxalate of lime are thrown down. According to Scherer there is a formation of lactic and acetic acids due to decomposition of the pigment under the influence of a mycodermic ferment analogous to the *mycoderma cerevisiæ*. Later on, the ammoniacal fermentation sets in from the presence of another ferment formed by the *micacterculus ureæ* of Cohn. The urea then combines with water to form carbonate of ammonia; the urine becomes paler, and soon deposits crystals of phosphates and the earthy oxalates, with urate of ammonia, and the ammonia-magnesian phosphate. It has been conclusively demonstrated that this fermentation does not go on in the bladder when the access of germs from the external air is shut off (Cazeneuve and Livon). Musculus has succeeded in separating from ammoniacal urine a soluble ferment (*ferment of urea*) which decomposes urea into carbonic acid and ammonia; this ferment is probably produced by the inferior organisms above mentioned.

The urinary sediments (omitting those occurring in pathological conditions) may be divided into (a) the *sediments of acid urine* and (b) *sediments of alkaline urine*. The first, when *crystalline*, may be formed by uric acid, oxalate of lime, and cystin (very rarely), all of which are easily recognised under the microscope; when *amorphous* they are formed either by urates and disappear by heat, to reappear on cooling of the urine, or phosphates of lime, which are dissolved on addition of an acid, but do not disappear on boiling. The second class of sediments, when *crystalline*, are due to the presence of acid urate of ammonia, and ammonia-magnesian phosphate, both of which are soluble in acids without effervescence, or to carbonate of calcium, which effervesces with acids; all these are recognisable under the microscope. The phosphate of magnesia sometimes accompanies the ammonia-magnesian phosphate. When *amorphous* this class of sediments are formed by the tribasic phosphate, or by the carbonate of calcium. Neutral

or feebly acid urines sometimes present crystals of the neutral phosphate of calcium.

The following analyses of urine are (1) by Vogel, who gives the mean of a number of analyses of the urine of several individuals, and (11) by Kerner, who gives the mean of the analyses of the urine of a man of 23 years during 8 days :

	I.		II.
	In 24 hours	In 1000 parts of urine	In 24 hours
Quantity of urine . . .	1,500.00	1,000.00	1,491.00
Water	1,440.00	960.00	—
Solids	60.00	40.00	—
Urea	35.00	23.30	38.10
Uric acid	.75	.50	.94
Chloride of sodium . . .	16.50	11.00	16.80
Phosphoric acid	3.50	2.30	3.42
Sulphuric acid	2.00	1.30	2.48
Earthy phosphates . . .	1.20	.80	1.35
Ammonia	.65	.40	.83
Free acid	3.00	2.00	1.95

Urea.—The daily amount of urea is about 34 grammes (22—43). It varies with many conditions. The proportion is greater in infancy, and diminishes with advancing years. The quantity is, as a rule, in proportion to that of the urine, and is found to be greatest in the afternoon and least in the morning. The greatest influence is that exercised by *alimentation*; the urea increases after a meal, attains its maximum at the end of six hours, and then diminishes. This increase is in proportion to the richness of the food in nitrogen. Under the influence of a food very rich in nitrogen, the daily quantity of urea may reach as high as 90 grammes, while it may sink to 20 grammes on a purely vegetable diet. The influence of exercise on the quantity of urea eliminated has been much disputed, but the conclusion generally arrived at now is, that although it hardly exercises any influence during moderate exertion, the amount is markedly increased during fatigue. According to Haughton and Byasson, cerebral activity increases the quantity of urea; sleep produces the opposite effect. During menstruation it is diminished, and that diminution which begins one or two days before, continues for some days after the cessation of the discharge. It is increased by the ingestion of water, of chloride of sodium, of nitrogenous substances (urea, uric acid, glycocoll, &c.); of ammoniacal salts, of nitrous oxide (E. Ritter), by transfusion (Landois), by injection of sugar into the blood (Richet and Moutard-Martin); it is diminished under the influence of antimonials, of arsenious acid, of phosphorus (E. Ritter), of quinine (V. Boeck), of iodide of potassium (Rabuteau), of turpentine, digitalis, ether, tobacco, carbonate of soda, &c. The action of tea and coffee is controverted; according to Roux the quantity of urea is diminished, while Hammond affirms that these substances have no influence.

Uric Acid.—The daily amount of this substance eliminated is about .6 grammes (.5—8); it is somewhat less in the female. At birth the urine con-

tains a larger proportion than in the adult. Food exercises a marked influence on the excretion; with an animal diet its quantity may be as much as 1 or 1.5 grammes per diem, while it falls during a vegetable diet to .3 gr. After food, the quantity is greatly increased; it then falls, and remains constant till the following meal. It is absent in the urine of herbivora, where it is replaced by hippuric acid. The influence of muscular exercise has not been determined. Sulphate of quinine, in large doses, diminishes the quantity (Ranke). It is so with the chloride of sodium, carbonate and sulphate of soda, iodide of potassium, caffeine, inhalation of oxygen, of nitrous acid (E. Ritter), also after imbibition of large quantities of fluid (Genth). It increases under the influence of antimonials, of arsenious acid, of phosphorus, of carbonic oxide (E. Ritter). Accordingly there is no definite parallelism between the elimination of urea and that of uric acid, as was formerly believed to exist. The proportion of uric acid to urea is 1:36 with an animal diet; 1:27.5 with a mixed, and 1:22 for a vegetable diet (Ritter).

Hippuric acid.—According to some authorities, this substance is always present in human urine, even during the use of an exclusively animal diet. This assertion is, however, questioned by most authorities. A small proportion is present in ordinary circumstances especially after the ingestion of certain vegetables (asparagus, myrtle-berries, plums), &c. It appears in large quantities after the ingestion of benzoic, quinic, or cinnamic acid. It is present in the urine of the newly-born fœtus during the first day. It is present in large proportion in the urine of herbivora. According to Weismann, this proportion diminishes when the processes of nutritive disassimilation are accelerated, and when the amount of carbonic acid eliminated by the lungs increases.

Creatinin.—The daily quantity of creatinin eliminated by the kidneys is about .5—1.3 grammes in the adult (in the female the amount is a little less). The urine of the infant, while nourished on milk alone, does not appear to contain it. The proportion increases with that of the meat ingested; by inanition it undergoes a marked diminution.

Other Nitrogenous Substances.—*Xanthin*, according to Neubauer, exists in the normal urine (.003 per 1000). *Oxaluric acid* exists in greater quantity in the shape of oxalurate of ammonia. *Allantoin* is found during the first few days of extra-uterine existence; it has also been found during pregnancy, after the ingestion of large quantities of tannin, or the use of food very rich in meat. *Cystin* is sometimes present, but the cause of its occasional presence has not been determined. Some other nitrogenous substances (so-called *nitrogenous extractives*) are present in variable amount, but the exact quantity is difficult, if not impossible, to define.

B. *Non-nitrogenous substances.*—*Oxalic acid* (in the form of oxalate of lime) is present in the urine in very small proportion (up to 20 milligrammes per diem). The quantity increases after the ingestion of any substances which contain oxalates, or those which yield them by oxidation such as citric acid. According to Szczerbakow, the presence of oxalic acid is always due to the decomposition of some pre-existing substance (oxaluric acid, or some similar compound).

Lactic (sarcolactic) acid is formed in the urine after severe muscular exercise; and, according to Brücke and Lehmann, it is a normal constituent. The normal existence of *sugar* in the urine has been greatly disputed, and

the discussion still remains unsettled; it has been admitted by Brücke, Blot, Bence, Jones, &c.; while it has been as vigorously denied by Friedlander, Seegen, and many other authorities. A distinctly appreciable quantity is sometimes present in the urine during lactation, especially if obstruction to any of the ducts has occurred. *Inosit* has sometimes been met with in diabetic urine instead of *glucose*, and was found in healthy urine by Strauss and Kulz after drinking large quantities of fluids. *Succinic acid* has been found in the urine after a meal rich in meat and fat (Meissner), also after the ingestion of asparagus, or alcohol.

C. *Sulpho-conjugate acids*.—*Indican* is found, in variable quantity, in human urine. It is increased by anything that prolongs the stay of the nitrogenous food in the alimentary canal. Animal food, ingestion of indol, or ligature of the intestine, increases the amount. The daily quantity in man .3-20 millogrammes of indigo. It may be present in the urine of carnivora, even during inanition, although in very small quantity; but, as a rule, it is absent in that of herbivora, except for certain kinds of food (in case of the rabbit it appears after ingestion of a large quantity of fresh herbs). In some, however, such as the horse, it is normally present in considerable quantity. The *phenolsulphates* form about a tenth of the sulphates of human urine; according to Brieger the daily excretion of *phenol* is about .003—.028 grm. This quantity increases during the use of a vegetable diet, after the ingestion of phenol, of tyrosin, benzol, indol, &c. They are more numerous in the urine of herbivora. *Chresosulphuric acid* usually accompanies the one last named. *Sulphopyrocatechic acid* is found only in exceptional circumstances.

D. *Coloring matters*.—*Urobilin* is present in about a tenth of the cases of normal urine examined; usually we find but its chromogen, which gives no spectroscopic band, but gives rise to the formation of urobilin by oxidation. Urobilin exists in large quantity in febrile urine. Thudichum has described another pigment, *urochrome*, which he regards as the normal coloring matter of urine, and which, being oxidised on exposure to the air, forms *uroerythrin*, which often gives the red tinge to deposits of urate of soda.

E. *Inorganic substances*.—*Chloride of Sodium*.—Of this substance the daily urine contains about 11.5 grammes (10—16). It presents great varieties in individuals; the proportion is smaller in women, and smaller still in children. Its excretion presents two maxima: one in the morning; the other in the afternoon. The quantity falls very low during fasting, but it never disappears completely: it is increased after food (especially after meat), also by drink, by ingestion of common salt, or of salts of potash, by muscular exercise, by mental work; it diminishes during sleep. *Phosphates*.—The daily quantity of phosphoric acid eliminated averages about 2.8 grammes (2.5—3.5); the great bulk of this being united with lime and magnesia. The maximum quantity of phosphates falls in the afternoon, after which the proportion diminishes during the night, and reaches a minimum in the morning. The amount is increased by food, and especially by an animal diet, by alcoholic drink (wine, beer), by muscular exercise, by the ingestion of phosphates, of alkaline carbonates, stimulating condiments, &c. According to Edfelson, there is a parallelism between the elimination of phosphates and that of the nitrogen of the urine. The phosphates are diminished in mania, and other forms of mental alienation (Mendel); and in epileptics, in the intervals between the attacks. The elimination is also diminished during

pregnancy; and in early life (during the period of growth) the proportion smaller than in the adult.

Variations in the Composition of the Urine.—(1) *According to the different states of the organism.* *Age.*—During the first 10 days of extra-uterine life, the quantity of urine is represented by the following figures (Martin and Ruge):

Days	1	2	3	4	5	6	7	8	9	10
Cubic centimetres	12	12	23	39	35	55	51	55	31	61

The reaction, according to the above authorities, is feebly acid; neutral, according to Parrot and Robin. The density and percentage of solids diminish from the first to the tenth day, with the single exception of the phosphoric acid, which increases. The urine of the first five days is turbid with mucus—corpuscles, epithelial scales, and urates. The density gradually increases, till the normal specific gravity is attained. The proportion of urea again diminishes in old age (even to one-half). *Sex.*—In the female, the daily quantity of urine and the proportion of solids are habitually less than in the male.

(2) *Functional variations.*—*Alimentation.*—Drinking increases not only the quantity of water separated by the kidneys, but also the salts, while there is no absolute change in the amount of urea and uric acid. On this account there is a relative diminution of the latter constituents. Animal food makes the urine acid, and increases the quantity of urea, and of uric acid; also of creatinin, sulphates, phosphates, and chlorides. A vegetable diet makes the urine alkaline, causing at the same time an increase of hippuric acid, oxalic acid, carbonates of potash, and soda (with glucose in case of a saccharine diet). Inanition makes the urine of herbivora acid, and the hippuric acid is then replaced by uric. *Digestion.*—The influence of this process on digestion we have already seen. The urine passed about three hours after digestion is dense, colored, less abundant, and presents variations in the quantity of its solids which have been already referred to. *Sweat.* The cutaneous secretion and that of the kidneys maintain a certain equilibrium; so that when one increases, the other diminishes. The increase of the urine, however, affects the water only. The influence of *muscular exercise* has been greatly disputed. The acidity increases (from increased formation of lactic acid); at the same time the uric acid diminishes: the creatinin appears unaffected. The chlorides, sulphates, and phosphates are increased, at least under certain conditions. The influence on the secretion of urea has been already discussed. *Mental work* causes, according to Byasson, an increase of urea, of phosphates, and of chloride of sodium, while the quantity of uric acid is diminished; his results, however, require confirmation. *Sleep* diminishes the quantity of urine; the quantity of urea, of sodium chloride, and of sulphates is also lessened. According to Kaupp, the phosphates are increased, but this is contradicted by Beaunis. *Pregnancy.*—The urine of pregnancy is less dense, and more aqueous, while its acidity is less, and it more easily undergoes the ammoniacal fermentation. Small traces of albumin, of glucose, and of allantoin may be present. *Kiæstin (gravidine)* which was formerly regarded as symptomatic of pregnancy, has been found to be merely an iridescent pellicle formed by crystals of ammonia-magnesian phos-

phate, mingled with microscopic fungi. During lactation sugar of milk (*lactose*) is often present.

Variations due to external causes.—Daily variations.—These depend in a great measure on the ingestion of food and drink; but the researches on the subject have shewn, during inanition, maxima and minima which almost exactly correspond with those observed under the ordinary conditions. *Temperature.* Elevation of the external temperature diminishes the quantity of urine, which becomes more concentrated; the urea and chloride of sodium are also diminished. *Passage of substances into the urine.* The metals and the insoluble metallic salts do not appear in the urine; a certain number of alkaline salts are found unaltered (carbonates, sulphates, borates, nitrates, silicates, chlorides, iodides, and bromides); ferrocyanide and sulphocyanide of potassium; the soluble salts of antimony, bismuth, arsenic, mercury, silver, and gold; oxalic acid, phenol, pyrogallie acid; biliary acids, urea, creatinin; morphia, quinine, strychnine, caffen, &c.; many coloring matters (carmin, logwood, camboge); santonin, sugar, and alcohol also appear in part.

The salts of the organic acids are found in great part in the state of carbonates; hyposulphites and sulphides in the form of sulphates; tannic acid as gallic; malic acid in the form of succinic; iodates and bromates are changed to iodides and bromides. Some substances, after ingestion, combine with others pre-existing in the body to form new compounds which are eliminated by the kidneys; an example of this is found in benzoic acid, which is changed in the system into hippuric.

The blood-pressure has a very important influence over the urinary secretion. The arrangement of the blood-vessels has been already described. The smaller size of the *vas efferens*, and its breaking up into capillaries, insures a pressure within the *Malpighian tuft* much above that of the general systemic capillaries. The arrangement of the capillaries within the tuft, also influences the circulation. The efferent vessels commence in the centre of the plexus, while the afferent capillaries are situated at the periphery, so that an increase of pressure in the afferent vessel has the effect of favoring the exit of the blood by the efferent vein, while an increase of the pressure within the latter vessel compresses the peripheral capillaries, and retards the circulation in the glomerulus. Also, as Ludwig has shown, the tubuli uriniferi are not intimately related to the capillaries, excepting at the level of the glomerulus, but are separated by lymph-spaces, the repletion of which has the effect of compressing both the capillaries and the tubes. Also, the disposition of the vessels and tubes in the boundary layer is such, that repletion of the vessels causes compression of the canals, and repletion of the canals causes compression of the vessels. Having regard to these facts, we can easily understand why it is that the quantity of urine is increased by increased activity of the heart, by diminution of the total calibre of the vessels (as by contraction *a frigore* of the cutaneous vessels, ligature or compression of the large arteries, &c.), by increase of the total quantity of blood (as by large draughts of fluid, injections of water into the veins, &c.); and why it is diminished by the opposite causes, diminished activity of the heart, stimulation of the pneumogastrics, effect of heat on the skin, abundant sweats, &c.

The solids of the urine are also increased by elevation of the blood-pressure, but not in equal proportion.

The state of the blood has not less influence. The constituents of the urine are found to vary continually with those of the blood, which are at once

influenced by the proportion of fluids, and also by the various products of digestion, which are taken into the circulation.

Origin of the Urinary Solids.—*Urea.* That the greater part of the urea is formed without the kidney has been conclusively proved by the experiments of recent years—the blood of the renal vein contains less urea than that of the artery (Picard, Gréhan), and, after extirpation of the kidneys, urea accumulates in the circulation (Voit, Meissner, Gréhan, &c.) The last assertion has been disputed by Oppler and Zalesky, but is now generally admitted by physiologists. The same accumulation occurs after ligature of the ureters. Some still admit the production of a portion of the urea in the kidney. Rosentein tried to settle the question by extirpation of one kidney, but after this operation no change in the quantity of urea was discovered.

Voit places the seat of its formation in the muscles, which, he observes, contain, in cholera, more urea than does the blood. Picard has advanced the same opinion, and has found that the muscles, especially during digestion, contain more urea than the blood, liver, or brain, while the latter organs contain more than is present in the blood. He believes that during digestion there is a formation of urea in the muscles, brain, and liver; whilst during inanition it is produced only by the muscles and brain.

Some authorities (Addison, Fuhrer, Ludwig, &c.), believe that the urea comes from destruction of the red blood-corpuscles, and Landois explains in this way the increase of its amount after transfusion. The spleen is believed by Gschleiden to be one of the seats of the formation of urea, as the quantity present in that organ always represents a greater proportion than that of the blood. The balance now seems, however, to be in favor of the idea that urea is derived from the disassimilation of albuminoids in all parts of the organism, but mainly in the tissues and organs just named.

Uric acid. The place of the formation of this substance is not definitely known. Zalewski asserted that it was in the kidney, for he found that after ligature of the ureters in birds and reptiles, deposits of uric acid were formed in the kidneys and other organs, while after nephrotomy these were not present. According to him, uric acid is not present in the blood in the normal state. Meissner has, however, by more delicate means of analysis, demonstrated the presence of small quantities. Pawlinoff has

also found that, after deligation of the ureters, the deposits of uric acid are found in the other organs, but not in the kidney ; which conclusively shews that the latter cannot be the seat of its formation. According to Meissner, the chief seat of its formation in birds and reptiles is the liver, whilst this organ in mammals forms urea. The relations of uric acid with guanin, sarcin, xanthin, and the existence of these substances in the liver, pancreas, spleen, thymus, and muscles (sarcin, xanthin), point to these organs as the great seats of formation of the uric acid which is eliminated by the kidney. Ranke makes the great seat of its manufacture to be the spleen, arguing from the facts that quinine in large doses diminishes the quantity of uric acid, and that a proportional increase of uric acid is found in splenic leukæmia. But, on the other hand, extirpation of the spleen causes no increase of the uric acid of the renal secretion (Cl. Bernard), and excepting the cases above mentioned, other splenic affections do not seem to affect the quantity of uric acid. Other observers suppose the source to be decomposition of leucocytes (leukæmia) or of the connective-tissue elements (gouty deposits). According to Pawlinoff, the uric acid exists in the blood in the form of the neutral urate of soda, which is much more soluble than the acid salt; this salt is easily decomposed by the carbonic acid of the tissues, and changed into a less soluble one, which is precipitated.

Hippuric acid. The sources of this substance have been already discussed. The chief seat of its formation is probably the kidney, but it is not the only one, for in the rabbit, after extirpation of both kidneys, hippuric acid was found to collect in the blood, liver, and muscles (Salomon).

Creatinin. The place of its formation is undetermined. It comes from creatin, which is itself found in the muscles.

Sulpho-conjugate acids. The *indican* is now known to come from the indol which is formed in the intestine. The *phenol-sulphuric acid* probably comes from the same source ; the phenol being apparently derived from the tyrosin. Ingestion of the latter substance causes an increase of the urinary phenol, and putrefaction of the pancreas with tyrosin furnishes phenol. Where the latter combines with the sulphuric acid has not been made out. It is not in the kidneys, according to Baumann and Brieger, for, after ligature of the ureters, there is no accumulation of this substance in the urine.

Urinary pigment. The origin of the urobilin from bilirubin has been already discussed.

Acids of urine. The acidity of the urine, as already pointed out, is in inverse ratio to that of the gastric contents. In a dog with gastric fistula, the urine always becomes alkaline after washing out the stomach with water, and the same has been observed in man, in cases of gastriectasis which were treated with the stomach-pump.

Innervation of the kidney.—Very contradictory results have been obtained by different observers in studying the influence of the nervous system on the kidney. Section of the renal plexus has been found by Pincus to be followed by arrest of the secretion; Hermann has merely found slight albuminuria; Cl. Bernard and Eckhard, polyuria. According to V. Wittich the renal plexus contains *secretory* nerves which are found between the renal artery and vein, and *vaso-motor* nerves which accompany the artery. Destruction of the former merely produces slight albuminuria, while section of the latter produces degeneration of the gland (accompanied by much albuminuria). On the other hand, however, no alteration of the kidney has been found by Bert and Ranvier to follow section of the renal plexus. Section of the great splanchnic in the dog increases the urinary secretion (Bernard, Eckhard), while it causes at the same time congestion of the kidney (Vulpian); stimulation of the peripheral end causes contraction of the vessels (paleness) of the organ, and arrests the secretion. Section of other sympathetic branches has no influence.

Section of the cervical sympathetic is followed by diminution of the renal secretion (Peyrani), while stimulation causes a marked increase. Stimulation of the pneumogastric, below the diaphragm, has been found by Cl. Bernard to be followed (in some cases) by increased secretion. Section of the cervical portion of the spinal cord is followed by arrest of the secretion, produced by lowering of the blood-pressure; and this arrest takes place even after division of the splanchnics (Eckhard). Puncture of the floor of the fourth ventricle produces polyuria, which is accompanied by albuminuria, or glycosuria according as the point selected is higher or lower. This result occurs even after section of the splanchnics, but the polyuria immediately disappears on division of the cervical or dorsal spinal cord. Eckhard has found polyuria to follow stimulation of

the median lobule of the vermis in the rabbit. Eckhard believes that centres for the urinary secretion exist both in the brain and medulla oblongata, but Bidder found that destruction of the nervous centres in the frog (leaving the medulla oblongata) did not produce cessation of the secretion; so that it would seem that the centre is located in the last-named portion of the nervous system.

Micturition.—The urine secreted by the kidneys passes into the ureter, along which it is propelled into the bladder, partly by the *vis a tergo* which is produced by the pressure of the secretion, and partly by the contraction of the muscular walls of this canal. In observations on man, in cases of ectopia vesicæ, the urine has been seen to flow into the bladder, drop by drop, from either ureter alternately, and at regular intervals of about three-quarters of a minute. The contractions of the walls of the ureter pass from above downwards, at the rate of about twenty to thirty millimetres per second, and are, according to Engelmann, entirely independent of the nervous system.

The bladder gradually expands with the increase of its contents. The pressure of the fluid on the wall of the bladder suffices to maintain the closure of the terminal portion of the ureter as it lies in its substance. The *modus operandi* of the closure of the urethral orifice is not so clearly understood. Up to a certain limit the retention of the vesical contents is undoubtedly involuntary and unconscious. The seat of closure is in the prostatic urethra and not, as many have believed, in the membranous segment. This is shown in the cadaver by introduction of a sound into the urethra; no urine escapes till the instrument passes into the prostatic urethra. It is also shown in the living body, as the power of retaining the urine in the bladder is preserved after opening the membranous urethra by external urethrotomy. Incision of the prostate, on the other hand, is immediately followed by incontinence.

The closure of this segment of the tube is maintained by (*a*) the elasticity of the prostate, and (*b*) by the tonic contraction of its muscular fibres, which form a kind of sphincter. The first-named agent retains the urine in the bladder after death, and is sufficient even to resist a moderate amount of external pressure. In the female, the urethral orifice is kept closed by the peri-urethral muscular fibres and elastic tissue.

During the time that the urine remains in the bladder it probably undergoes some changes of composition. According to Kaupp it becomes more concentrated; according to Treskni, it absorbs water and loses a little urea.

So long as the contained urine is small in quantity the elasticity of the prostate, above referred to, suffices to prevent the escape of any of the fluid into the urethra. When a somewhat larger quantity is collected, the irritation of the sensory nerves, which is carried up to the cord, causes a reflex contraction of the involuntary muscular fibres which surround the prostatic urethra. The presence of a larger quantity next causes a reflex contraction of the muscular fibres of the walls of the bladder, which forces a small quantity of urine into the prostatic urethra. A peculiar sensation is then felt, the desire to micturate (*besoin d'uriner*), and, if it be necessary to retain the vesical contents still longer, the contraction of the voluntary muscular fibres which surround the prostatic and mem-

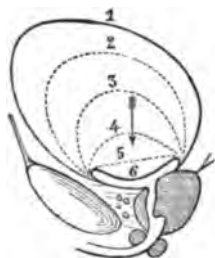


Fig. 65. (After Küss).

Diagram of Bladder during Micturition. 1. Bladder fully distended; by the contraction of its own fibres its walls are made to assume successively the positions 2, 3, 4, 5. The pressure of the abdominal viscera forces it into the form represented by 6, where it forms a dome with the concavity upwards.

branous portions of the urethra is called into play, and we are conscious of an effort which prevents the escape of the urine. But if the bladder become extremely distended, the irritation of the sensory fibres of the mucous membrane becomes so great that it inhibits the spinal centres which preside over the movements of the neck of the bladder, and the urine is allowed to escape even against the will. If, on the other hand, the desire is acceded to at once, the sphincter is allowed to relax while the muscular walls of the bladder contract and expel its contents. At the commencement of voluntary micturition there is always a slight effort with the glottis closed (Küss); and, at the close of the act, another effort is necessary to expel the last few drops

of urine from the bladder and along the urethra. The contraction of the surrounding involuntary muscular fibres, and of the accelerator urinæ muscle, has the effect of emptying completely the urethral canal.

The nervous *centre for micturition* is found in the lumbar portion of the spinal cord (Goltz).

Tonicity of the Sphincters.—According to some authorities (Rosenthal, V. Wittich, &c.) the sphincters have no tonicity derived from the nervous system, and the permanent occlusion of the vesical and rectal orifices is due merely to the elasticity of the surrounding tissues. In favor of this idea they bring forward the fact that after death, and before rigor mortis has set in, the rectum and bladder are able to retain their contents against a pressure at least equal to that to which they are subjected during life. Heidenhain and Colberg have been led by their experiments to admit the existence of a tonic contraction, involuntary and continuous. By narcotising an animal, introducing a manometer into the urethra, and then making pressure till the first drop of urine appeared; then destroying life by the action of prussic acid or by hæmorrhage, and again making pressure, it was found that less weight was required in the latter case. These experiments have been repeated by Gianuzzi, Nawrocki, and others, and the results confirmed. According to Gianuzzi, this tonicity is of reflex origin, for he has found that after section of the posterior roots of the spinal nerves, the sphincters (rectal and vesical), became partly relaxed. Against this, however, is the fact that narcotism, which diminishes the reflex irritability of muscle, does not diminish the tone of the sphincters.

CHAPTER XVII.

VOICE AND SPEECH.

THE upper segment of the wind-pipe is specially modified for the production of voice. This portion of the air tube (*larynx*, voice-box), transmits the air without any formation of sound beyond a slight *soufflet*; but when the walls or the tube have undergone certain modifications by the action of its muscles the passage of the current of expired air is accompanied by the production of voice. The seat of the formation of vocal sounds has been shown by careful examination to be at the inferior laryngeal ligaments (*true vocal cords*).

Methods of observation.—(1) *In the dead body.*—By experiments made on the cadaver, Terrain was the first to show that the production of voice was due to the vibration of the true vocal cords. His experiments were repeated and extended by many others, especially J. Muller, who made many valuable observations. (2) *Artificial larynx.*—This is used in nearly the same way as that of the dead body. (3) *Vision.*—After incision of the thyro-hyoid membrane, the epiglottis is drawn forwards and the rima glottidis exposed to view. (4) *Laryngoscopy.*—Garcia, the singer (in 1854), was the first to apply the mirror for the purpose of observing the interior of the human larynx during life. This mode of examination has been perfected by Czermak, Turck, and others. Hirschberg has employed means of enlarging the image and changing its position. Oertel has adopted the intermittent form of illumination (*laryngostroboscopy*).

The *rima glottidis*, where the vocal sounds are produced, consists of two functionally separate parts; an anterior (*glottis vocalis*) placed between the true vocal cords, and a posterior (shorter) portion, *glottis respiratoria*, placed between the arytnoid cartilages.

The true vocal cords, on the vibration of which the production of voice depends, are formed almost entirely of yellow elastic tissue. They are attached in front in the retiring angle of the thyroid cartilage, and behind to the tubercle on the front of base of arytnoid. Accordingly, any change in position of either of these cartilages has a definite influence on the position, tension, &c., of the vocal ligaments, and, consequently,

on the production of voice. The muscles which have a direct influence on the vocal cords are (as usually described in the anatomical text-books), the *crico-thyroideus*, *thyro-arytænoides*, *crico-arytænoides posticus*, *crico-arytænoides lateralis*, and *arytænoides proprius*. The latter is an azygos muscle; all the others form symmetrical pairs. The actions on the vocal cords are as follows :—

Crico-thyroideus makes tense ;

Thyro-arytænoides relaxes ;

Crico-arytænoides posticus separates (opens glottis) ;

Crico-arytænoides lateralis approximates (closes glottis) ;

Arytænoides proprius approximates the arytenoid cartilages, and closes the respiratory glottis.

Conditions of the production of Voice.—(1) *Pressure of the current of expired air.*—To produce vibration of the vocal cords it is necessary that the current of air, in passing through the glottis, be under the influence of a pressure sufficient to disturb their equilibrium. This pressure has been measured by the introduction of a manometer into the trachea, and was found to represent that of 160 mm. of water for sounds of medium height, increasing to 945 mm. for the highest possible sound. In order to maintain the necessary pressure it is necessary that the air of the respiratory passages be compressed by the action of the muscles of expiration; and it is also necessary that it be not allowed to escape too easily. The latter element is maintained by the action of the laryngeal muscles, which narrow the glottis, so as to prevent too rapid escape of the expired air. Accordingly, when an opening is made in the trachea voice is immediately lost, as the easy escape of the expired air lowers the pressure beneath the indispensable minimum.

(2) *Tension of the Vocal Cords.*—For the production of vocal sounds it is necessary that these bands should be stretched in their length, breadth, and thickness. The tension in length is due to the separation of their anterior and posterior points of attachment; the tension in breadth is due to their approach to the median line; tension in the vertical direction is maintained by contraction of the inner bundle of the thyro-arytænoid muscle. In this way the true vocal cords form distinct elastic bands, capable of vibrating along their whole length. The tension is increased during the expiratory act by the current

of escaping air, and the reason why it is that the voice cannot be produced during inspiration, excepting in rare instances, is simply that the pressure of the current of air entering the larynx is not sufficient to cause the necessary vibration.

Emission of Sound.—When the production of voice is about to take place, the glottis is narrowed, or completely closed, by the action of the muscles above indicated. The closure is produced by the approximation of the aryænaoid cartilages or of their vocal apophyses only; in the former case it extends along the whole length, in the latter it engages only the vocal part of the glottis.

When the vocal cords have acquired the length and tension corresponding to the sound about to be produced, they are suddenly separated and thrown into vibration by the current of expired air. These movements can be easily seen by means of the laryngoscope. The vibrations engage nearly the whole thickness of both vocal cords, and they vary in number and amplitude with the various conditions to be afterwards considered.

The vibrations of the vocal cords alone can produce but feeble sounds, but the rapid and periodic shocks of the expired air at the opening of the glottis cause corresponding movements of the air contained in the pharynx and nasal fossæ. In the larynx, then, as in artificial wind instruments, it is the air which forms the sounding body, and the vocal cords merely regulate the periodicity and characters of the sound.

Characters of the Voice.—The *intensity* of the voice depends on the amplitude of the vibrations of the vocal cords, and, consequently, is dependent on the force of the current of expired air. The intensity of the laryngeal sound is reinforced by the resonance of the masses of air contained in the supra- and sub-glottic cavities, and by the vibrations of the walls of these cavities.

Height of the Sound.—The height of the sound depends on the number of vibrations of the true vocal cords, and of the air which is set in motion by them. The more rapid the vibrations the more acute is the sound. The conditions which most influence the height of the sound are the length, breadth, and above all, the tension of the true vocal cords. These bands are more tense in the elevated sounds, less so in the grave.

The force of the current of air has also a considerable influ-

ence on the height of the sound. J. Müller found in his experiments that by increasing the force of the current of air, without altering the tension of the vocal cords, he was able to raise the sound by a fifth. The length of the trachea and that of the supra-glottidean cavities (pharynx, *lc.*), has no influence on the height of the sound. The ascent of the larynx, which is observed in high sounds, is a simple accessory phenomenon, and has no essential importance in the production of sound. Whether this ascent is due to the pressure of the air alone, or to the action of the elevator muscles of the hyoid bone, is a question still undecided.

The medium range of the human voice is the length of two octaves. By practice it attains a range of about two and a-half octaves, and, in exceptional cases, even three or three and a-half, as in the instance of the celebrated singer Farinelli. Nilsson attained the *fa* of the fourth octave, and Mozart speaks of a female singer, Bastardella, who reached to *do* in the fifth octave (corresponding to 2,112 vibrations).

We are familiar with two chief modifications of the human voice: (*a*) the so-called *chest voice*, which gives full, grave, voluminous sounds, and is accompanied by a resonance of the thoracic walls; (*b*) the *head or throat voice (falsetto)*, in which the vocal sounds are more shrill and acute in character, and produced especially in the upper part of the air cavities. In the former, the glottis is never completely closed, but presents an elliptical chink of varying width, being very narrow in the high notes, and more open in the graver sounds. In the falsetto voice, on the other hand, the respiratory glottis is closed, while the glottis vocalis presents an opening of considerable size, through which the air passes with sufficient ease. Also, for the same quantity of inspired air, the falsetto notes are not so long maintained as the chest notes (Garcia). According to Müller, the false vocal cords are applied to the true, so that the latter are prevented from vibrating, except along their free margins and median portion. Oertel, by the application of his method of laryngostroboscopy, has obtained different results; he found, in a practical singer, that, in a falsetto voice, the vocal cords vibrated along their whole length, but formed nodal points parallel to the free border, and swellings produced by the vibrations.

According to Michel, each register of the human voice has

a dominant muscle ; this, for the chest register, is the *crico-arytænoideus lateralis* ; for the medium register, the *thyro-arytænoideus* ; for the superior register (falsetto voice), the *crico-thyroid* and *thyro-arytænoideus* muscles are both completely relaxed. The falsetto voice is accompanied by resonance in the pharyngeal, nasal, and buccal cavities.

Second, from the results of his experiments on cats, was led to regard the falsetto voice as being essentially the result of vibration of the false vocal cords. According to Petrequin, the glottis in this case merely performs the functions of the opening of a flute, and the air alone enters into vibration ; the vocal cords no longer acting as elastic strings.

Timbre of the Voice.—This depends, as does the timbre of sound, on the number and intensity of the harmonics. The laryngeal sound is a complex one, formed of one fundamental note and a number of harmonics ; Helmholtz has determined the existence of six or eight clearly perceptible, but they are not so distinct in case of the human voice as in other instruments. The proper laryngeal sound is, however, greatly modified by the resonance of the supra-glottic cavities, and especially in that of the mouth ; the different harmonics are modified by the various positions of the mouth, which alter very considerably the timbre of the voice.

Two kinds of timbre are distinguished : the *clear* and the *dull* (*sombre*). In the former, the larynx is elevated, the trachea lengthened, the supra-glottic spaces shortened, and vocalization more easy for the vowels *e* and *i*. In the latter the larynx is lowered, the trachea is shortened, and the supra-glottic funnel elongated, the buccal opening is narrowed, and the first harmonics of the fundamental laryngeal sound are reinforced. Vocalisation is more easy for the vowels *o* and *u* ; that of the letter *a* is equally easy for both kinds of timbre.

Maintenance of the Sound.—In order that the production of vocal sound be kept up for some time, it is essential that too easy an escape should not be allowed to the current of expired air, otherwise the pressure diminishes too rapidly, and the vocal cords would soon cease to vibrate. The opening of the glottis must be kept narrow, and a certain equilibrium maintained between the action of the expiratory forces, for the regulation of the quantity of escaping air.

To maintain a certain degree of *intensity* it is necessary that

the pressure of the expired air remain equal throughout the time of the emission of the sound, so that the amplitude of the vibrations undergoes no variation; and as the quantity of air in the trachea and bronchi diminishes gradually with the emission of sound, the expiratory muscles must increase the force of their contractions to maintain the constant pressure.

To maintain the *height* of the sound, the mechanism is different, for as the tracheal pressure gradually diminishes, the height of the sound must be sustained by a compensatory increase of tension of the true vocal cords. The *flexibility* of the voice depends on the rapidity of the changes of tension of the true vocal cords.

Influence of age.—In infancy the voice is shrill, and up to the age of six, has a range of not more than an octave in extent. Up to puberty, the characters of the voice are the same in both sexes, but at this period the voice of the male “breaks,” and acquires a lower pitch, from congestion and sudden increase of development of the true vocal cords. During this period of congestion (*mu* of the French writers), the voice is extremely rough and guttural, and, after this period has past, the voice is found to have fallen an octave in pitch in boys, and two tones in girls, while it has, at the same time, undergone notable changes in timbre and in intensity. In old age, it again changes; the intensity diminishes, the diapason falls, the timbre alters, and the voice becomes tremulous. **Sex.**—The female voice is always less intense, more flexible, and of different timbre to that of man. That part of the musical scale which reaches from the *sol* of the lower octave to the *si* of the second is common to both voices. The female always sings in the octave of the male voice. The voice of *castrata* approaches the characters of the infantile voice, but with greater amplitude and development.

The varieties of the male voice are: bass, barytone, tenor; of the female, contralto, mezzo-soprano, and soprano. The several meanings of these terms are well known.

The voice of *ventriloquists* is *not* produced, as some authors have believed, during the inspiratory act (Sigond); it is formed, like the ordinary voice, during expiration, but with changes of intensity, timbre, &c., which, combined with the movements and expression of the ventriloquist, modify completely the normal characters.

Speech.—Speech is made up of *articulate words*, each of which is formed by a compound sound partly produced in the larynx and partly in the accessory vocal cavities (pharynx, mouth, &c.). In ordinary speaking (articulate speech) the sound is produced at the glottis vocalis. In whispering, on the other hand, the only laryngeal sound is that produced by the friction of the air passing through the respiratory glottis, the glottis vocalis remaining closed.

Of late years several methods have been devised for registration of vocal sounds. The chief instruments employed are : the *phonautograph* of Scott, the *phonograph* of Edison, and the *manometric flames* of Koenig. A full description of these instruments here would occupy too much space ; they may be studied in special treatises. The phonetic movements of the lips, soft palate, and larynx have also been registered by means of the apparatus of Marey and Rosapelly. To analyse the various sounds the *ear* also may be employed, as many prefer, or *tuning-forks*, of various lengths, may be used, or the *resonators* devised by Helmholtz and Auerbach. In studying the movements of the tongue, direct inspection may be resorted to, or the introduction of the finger into the mouth, so as to feel the different degrees of pressure. The best plan, probably, is that of coloring the surface of the tongue, which then leaves its impression on those parts of the palatine and superior dental arches which come into contact with its surface during articulation (Oakley Coles, Grützner).

The researches of Kempelen, Kratzenstein, and Willis on the artificial production of articulate sounds have also thrown a flood of light on the subject, and more scientifically accurate results have been since obtained by Helmholtz. The most perfect apparatus which has yet been devised for the reproduction of the human voice is the phonograph of Edison.

The elementary articulate sounds are divided into vowels and consonants.

Vowels.—These are the sounds formed in the larynx, and of which the harmonics are reinforced by the resonance of the supra-glottic segment of the air-passages. Accordingly, as the vowel-sounds undergo modifications with every change of shape of the buccal cavity, there is a possible infinity of these sounds. Among these, however, there are certain primitive vowels which are found in nearly all languages, and of which the ear readily distinguishes the characters.

In the production of each of these sounds, the buccal cavity assumes a characteristic form. No current of air passes through the nose, as the posterior nares are shut off by the soft palate. In the vowel sound *i* (ee as in feet), the tongue is elevated, and separated from the soft palate by a narrow isthmus ; so that the buccal cavity has the form of a short broad flask with a narrow neck. This is the highest vowel sound, and is, according to

Helmholtz, formed by two sounds, of which one is produced in the neck, and the other in the belly of the flask. In *u* (oo) the buccal cavity forms a flask of rather narrow, rounded form, with little or no neck. This is the lowest of the vowel sounds. For the production of *a* (as in father), which is intermediate between the other two, the lips are separated more or less widely, and the buccal cavity forms a funnel with the apex backwards. Some authorities look upon this as the *primitive vowel*, par excellence, from which all the others diverge. With *e* (short), the shape of the mouth is similar to that described for *i*, but somewhat longer. For *o* the buccal cavity is flask-shaped, with lips closer than for *a*, and somewhat protracted so as to elongate the sounding-tube.

Consonants.—These are the sounds formed in the additional sounding-tube, and reinforced by the laryngeal sound. In these sounds certain mobile parts of the additional tube are contracted, so as to form a temporary glottis, which is susceptible of producing a sound during the passage of the current of expired air.

Consonants have accordingly been classified according to the region of their formation. They are also grouped according to the character of the movements which give rise to them. The following table gives both modes of division :—

REGIONS OF ARTICULATION.

				Labial.	Lingual.	Guttural.
Continuous	{	Hard	.	F.	S.	CH.
		Soft	.	V. W.	SCH. Z.	J.
Explosive	{	Simple {	Hard	P.	T.	K.
		Soft	.	B.	D.	G.
	{	Aspirate {	Hard	PH.	TH.	KH.
		Soft	.	BH.	DH.	GH.
Vibrating	.	.	.	R.	L.	R.
Nasal	.	.	.	M.	N. R.	N.

For the *continuous* consonants the additional (supra-glottic) tube is merely narrowed, and the production of the sound lasts as long as does the passage of the current of expired air. For the *explosive* (*mute*) consonants, a momentary complete closure occurs in the region of articulation, and the production of the sound lasts but an instant, being formed either at the moment

of occlusion (aB), or the moment of opening (Ba). These consonants are always associated with the preceding or succeeding vowels. In forming the *vibrating* consonants, the constricted part of the additional tube is thrown into vibration by the current of expired air.

In the three preceding forms, the current of expired air passes through the mouth, the nasal fossæ being hermetically closed, but the soft palate is lowered in some cases for the purpose of allowing the escaping current of air to give special timbre to the so-called *nasal* consonants.

The union of articulate sounds leads to the formation of syllables, and syllables, in turn, when united, form words.

The articulation of words, as the production of voice, presents varying acoustic characters of intensity, duration, and intonation. The *accent* depends on the intensity of the sound, the *quantity* on its duration, the *intonation* which, in our language generally serves but to give variety to phrase, and emphasize certain passages, has in others a much greater importance, as it causes modifications in the sense of the same word.

CHAPTER XVIII.

THE SENSES.

THE five senses, or gateways of knowledge, by the aid of which we make ourselves acquainted with the nature and properties of external matter are : touch, taste, smell, hearing, and sight.

The first of these has been already studied at sufficient length in discussing the physiology of innervation ; the others shall now be taken in order.

TASTE.

The seat of taste (*gustatory sensation*) is in the base, point, margins, and median part of dorsal surface of tongue ; the under surface of the organ has no perception. Some observers also place the sensation in the velum pendulum palati, uvula, and anterior pillars of fauces, but the correctness of this is very doubtful. The base of the tongue is the most sensible region, especially to bitter tastes ; the tip best distinguishes sweet and acid tastes.



Fig 66. Filiform, fungiform, and calyciform papillæ.

The tongue itself is a muscular and very mobile organ, covered by mucous membrane, with compound scaly epithelium. There are numerous gland-tubes, the secretion of which moistens the surface of the organ, and a marked peculiarity is given to the surface by the presence of papillæ, which differ from those of other surfaces, in structure and arrangement. *Simple* papillæ, analogous to those of the skin, are present, but the characteristic ones are the *compound* papillæ, of which there are three varieties—(1) *filiform*, (2) *fungiform*, and (3) *calyciform* (*circumvallate*). They are all, however, formed by projections of the mucous membrane, containing terminal twigs of the blood-vessels and nerves, and the surface of each is studded by simple papillæ.

(1) *Filiform*.—These are the most numerous, and are distributed over the whole surface, especially on the median part of the dorsum. The thick coat of epithelium which covers each is prolonged from the surface in the form of hair-like prolongations. The use is probably mechanical, as they possess no gustatory sensation.

(2) *Fungiform*.—These papillæ (so-called from their peculiar shape), are scattered over the sides and tip of the tongue, and in fewer numbers over the median tract of the dorsum. The summit of each is broader than the base, and the surface is studded with simple papillæ.

(3) *Calyciform* (*circumvallate*).—These papillæ, eight or ten in number, are arranged in a V-shaped line at the base of the tongue; the apex being placed at the *foramen cecum* of Morgagni. Each is surrounded by a fossa or trench, from which structural peculiarity they are called circumvallate. This fossa is surrounded by an elevated margin, and the papilla itself has a central depression.

On the sides of the circumvallate papillæ peculiar structures (*taste-goblets*, *gustatory buds*), have been described by Schwalbe and Lövén. These minute bodies are oval in shape, and made up of closely packed masses of elongated fusiform cells. A single layer of broader (*encasing*) cells covers the surface. The central (*gustatory*) cells terminate in delicate hair-like processes which project on the fore surface. Similar structures have been discovered on the posterior surface of the epiglottis.

Varieties of gustatory sensations.—Some physiologists describe but two kinds of taste—the *sweet* and the *bitter*, and when

olfactory and tactile sensations are eliminated, there remain but these. In the ordinary conditions, however, two other kinds of taste are distinctly appreciable: the *acid*, and the *saline*. The nature of the sapid body does not in any way explain the sensation which it produces when applied to the nerves of taste; similar sensations are caused by substances, of which the chemical properties are totally different; for instance, sweetness is common to sugar, salts of lead, chloroform, &c.

The gustatory sensibility of the tongue is due to the calyciform and fungiform papillæ; if the tongue is touched with a sapid substance between the papillæ no sensation of taste, is elicited so long as the papillæ are not reached. The greater the number of papillæ brought into contact with the substance the more distinct is the sensation elicited.

It would appear that the sapid substances have to be dissolved in the buccal fluids, and pass in through the mucous membrane to the nerve-endings. Solid and gaseous substances are also able to awake gustatory sensations. After application of the sapid substance a certain interval elapses before the sensation is perceived, and this period is diminished by the movements of the tongue and pressure of the organ against the palatine arch, at the same time that the gustatory sensibility is increased by multiplying the papillary impressions. Saline tastes are the most rapidly perceived; bitter substances are slower to be made out.

Substances injected into the blood also produce gustatory impressions; if colocynth be injected into the veins of a dog the animal makes movements of mastication and of taste, as if this substance had been placed on the tongue. The bitter taste that exists in jaundice is an example of the same kind.

The delicacy of the sensation is different for the various kinds of gustation. The bitter substances allow of the greatest dilution; a solution of sulphate of quinine at 1 : 100,000 elicited the sensation of bitterness in 32 cases of 100 experimented on (Camerer). The temperature most favourable for the sensation is 10°—35° C. (50°—95° F.); a high or low temperature diminishes the perception.

Tactile sensations (*astringents*), and thermic sensations (*mus-tard*, &c.), are usually confounded with taste proper. It is the same with olfactory sensations; for instance, the taste of vanilla

is but an olfactory sensation. If the nose is held at the time, the sensation disappears.

The application of a constant current to the tongue causes, during the time of its passage, an acid taste at the posterior pole, and an alkaline, or, rather, an acrid taste at the negative ; these sensations do not appear due to decomposition of the buccal secretions.

The *nerves* of taste are the lingual branches of the glosso-pharyngeal and of the trifacial ; the former supplies the base of the tongue, and is specially connected with the sensation of bitterness ; the gustatory of fifth supplies the anterior two-thirds of the tongue, and is principally affected by sweet tastes ; after section of this nerve the sensation of sweetness is no longer perceptible (Michel). For the origin of the gustatory branches of this nerve, see page 360.

SMELL.

We are still ignorant of the nature of the properties, on the presence of which depend the power of eliciting the sensation of odor. We only know that the substance must be volatile, and that infinitely small particles suffice to produce stimulation of the olfactory nerves. The fragments of musk or of amber preserve their odor for years without perceptible loss of weight, and air containing a millionth part of sulphuretted hydrogen distinctly smells of this gas.

The seat of olfaction is in the upper part of the nasal fossæ, including the cribriform plates of the ethmoid bones, the upper third of the septum, and the corresponding portion of the outer wall (superior turbinated bone, upper half of middle, and superior meatus between). This tract of the mucous membrane is lined by cylindrical epithelial cells, between which are placed elongated fusiform cells (*olfactory cells* of Max Schultze), which send processes from one end to the free surface, and from the other to the mucous membrane to communicate with the terminal twigs of the olfactory nerve. In the region of the nostrils the nasal epithelium is squamous, while the so-called *respiratory region*, which occupies the greater part of the nasal fossæ, is lined by ciliated columnar cells.

Examination of the physical characters of odoriferous substances (*odoroscopy* of Prevost). The substances are all characterised by the rapidity with which their particles move about

over the surface of water, and also when placed on moist glass every odoriferous substance, solid or fluid, repels the water which it touches (Prevost). Liegeois adds two other characters—when the powdered substances are sprinkled on water they scatter themselves on its surface with extreme rapidity, each particle separating itself from the neighboring ones; also the movements of camphor and succinic acid cease, when an odoriferous body touches the surface of the water on which these substances float. If a small quantity of oil be spread on the surface of water it rapidly spreads itself over the whole surface, forming a pellicle made up of granular particles of extreme minuteness (.001—.004 mm. diameter). These granules are carried off by the watery vapor during evaporation. This is further exemplified by the fact that some substances, such as the fixed oils, which have no marked smell in the pure state, become odoriferous when placed in contact with water (Liegeois). It has long been known that the odor of flowers is much more distinctly perceived in the dewy morning, or when the atmosphere is charged with watery vapor, as after rain. It has been remarked by Tyndall, that most volatile odoriferous substances have a notable power of absorption by heat.

The atmospheric air is the vehicle of all odors, and transfers them to the olfactory mucous membrane; accordingly there is no smell perceptible under water, and even if the nasal fossæ be filled with eau de Cologne there is no olfactory sensation elicited. But an aerial medium alone is not enough; it is necessary that the air should be in motion, and that the current of air be in the proper direction. If the breath be held in an odoriferous atmosphere, no sense of smell is perceived; to give it all its intensity it is essential that the current of inspired air have a certain force, and come into contact with the edge of the inferior turbinated bone, which divides and sends it towards the olfactory surface. The sensation of smell produced by the current of expired air is barely appreciable; the same is found when the air is brought directly into contact with the mucous membrane, whether by means of a tube, or when the part is exposed by a surgical operation.

The intensity of the olfactory sensation depends on (*a*) the quantity of odoriferous particles, and (*b*) the number of nerve-fibres stimulated (or extent of surface). It is generally very transitory. The acuteness of the sense varies greatly in indi-

viduals, and may be cultivated to a high degree of development by attention and practice.

If different odors are applied simultaneously to the two nostrils there is no mingling of the two sensations; they are perceived alternately, but only one at a time.

The best *classification* of odors is that of Linnæus, who divided them as follows: *aromatic* (laurel), *fragrant* (lily), *ambrosial* (amber), *alliacous* (oil), *fætid* (valerian), *poisonous* (solanacæ), *nauseous* (gourd).

Consecutive olfactory sensations are sometimes perceived, and are due to the retention in the meatuses or sinuses of the nasal fossæ of particles of the odoriferous substance. They appear more frequent after disagreeable odors (cadaverous, &c.)

Subjective sensations are perceived by persons who are the subject of mental derangement.

Tactile sensations of the olfactory mucous membrane (produced by ammonia, acetic acid, &c.), should be distinguished from olfactory sensations proper, although in popular language they are confounded with the latter. They are really analogous to the tactile sensations produced, for example, when they are brought into contact with the ocular mucous membrane.

That the *nerves* of this sensation are the so-called olfactory nerves is now universally admitted by physiologists. (See page 350).

HEARING.

The ear, or organ of hearing, by the aid of which we become cognizant of sounds, is divided into three parts: external, middle, and internal. The *external* ear consists of the *auricle* (*pinna*), and the *external auditory meatus*. The *middle* ear consists of the *tympa-num*, with the bones, muscles, and ligaments contained within its cavity, and the Eustachian tube by means of which it communicates with the naso-pharyngeal cavity. The *internal* ear (*labyrinth*) comprises the *cochlea*, *vestibule*, and *semicircular canals*, and their contained structures, most of which are of marvellous complexity.

The *auricle* presents externally an irregularly concave surface, presenting a number of elevations and depressions, which have received rather fanciful names from descriptive anatomists. The external curved rim of the *pinna* is called the *helix*, inside which is the *fossa of the helix* (*fossa scaphoidea*), separating it

from the *antihelix*, which divides above to enclose the fossa of the *antihelix* (*fossa triangularis*). The central hollow is called the *concha*, at the lower part of which is the *fissura intertragica*, which separates the *tragus* in front, from the *anti-tragus* behind. The flexible dependent part of the auricle is called the *lobule*, the rest is strengthened by the presence of a layer of yellow fibro-cartilage, of which a folded process passes into the external auditory meatus, which it lines for the outer half inch of its length, leaving a deficiency above. The fissures which exist around the margin of the cartilage, of which this is the principal, are known as the *fissures of Santorini*.

The **external auditory meatus** is about an inch and a quarter in length. Traced from the outside it passes first upwards and a little backwards, then downwards, forwards and inwards, to its termination at the *membrana tympani*. Inside the cartilaginous prolongation from the pinna, the wall of the canal is formed of bone, with its cutaneous lining. The epidermis is prolonged over the tympanic membrane, of which it forms the external layer. The cutaneous glands in the external auditory canal resemble in structure the sudoriparous glands, but form a peculiar secretion, the *cerumen* (ear-wax), from which they are called the *ceruminous glands*. The hairs which grow at the outer opening of the canal (*vibrissae*) are useful in preventing the entrance of dust, insects, &c., and it is probable that the cerumen fulfils a similar function.

The *membrana tympani* is set in a groove in the bone, which presents a deficiency (*notch of Rivinus*) at the upper part. The corresponding part of the membrane is thinner and more yielding than the rest (*membrana flaccida of Shrapnell*). The membrane itself is set obliquely, sloping from above downwards and inwards, and forming with the floor of the external meatus an angle of about 45°. It consists of three layers: an external (*cuticular*) continuous with that of the cutaneous surface; an internal (*mucous*) derived from that of the tympanic cavity; and a middle (*fibrous*) the proper tissue of the membrane. The fibres of the latter are arranged in two ways: the external radiate from the centre, while the internal are disposed in an annular form.

The *tympanum* forms a very short and oblique section of a cylinder, the ends of which are placed externally and internally, and the roof wider than the floor. It communicates with the

naso-pharyngeal cavity in front by means of the Eustachian tube, and behind it opens into the accessory cavity of the mastoid cells.

The anterior (*cartilaginous*) part of the Eustachian tube is about three-quarters of an inch long, and formed of a triangular piece of yellow fibro-cartilage, folded upon itself so as to have the edges below, which are joined by dense connective tissue. The mouth is closed, except during the act of swallowing, when it is opened by the action of the fibres of the tensor palati which are attached to it. These fibres have, on this account, been called the *dilatator tubæ*. According to Rüdinger, however, a narrow chink remains normally open. Professor Cleland differs from other anatomists in holding the view that the Eustachian tube is always open, *except during the act of swallowing*, when it is closed by muscular action.

The tympanic cavity is crossed by a chain of bones named (in the order from without inwards) : *malleus*, *incus*, and *stapes*. The malleus (hammer) presents a *head*, *neck*, and three processes : *manubrium*, which passes downwards and inwards between the mucous and fibrous layers of the *membrana tympani*, the *processus gracilis* (of Rau), which passes forwards and outwards to lodge in the fissure of Glaser, and the *processus brevis* (vel *obtusus*) which proceeds for a very short distance outwards. At the junction of these with the neck of the bone are attached the following muscles respectively : *tensor tympani*, *laxator tympani*, and *laxator tympani minor* (Sömmering). The head of this bone articulates with that of the *incus* (anvil), and the body gives origin to two fang-like processes, which give the whole a much closer resemblance to a molar tooth than to an anvil. The shorter process (*crus breve*) passes backwards, to be attached, by a very short ligament, close to the opening of the mastoid cells ; the long process (*crus longum*) descends almost vertically to articulate with the head of the *stapes*. The latter bone, which closely resembles the object (stirrup) after which it is named, consists of a *head*, *neck*, two *crura* and a *base*. It is placed horizontally, with the base fixed by means of the annular ligament in the fenestra ovalis, on the inner wall of the tympanic cavity. Besides the ligaments already mentioned, there are delicate suspensory ligaments of the malleus and incus, and an anterior ligament of the malleus, which retain these bones in position. At the end of the long process of the incus, is an

epiphysis (sometimes separate even in the adult) called the *os orbiculare* (vel *lenticulare*). A number of openings are found on the walls of the tympanic cavity. In front: Eustachian tube, and canal for tensor tympani. Behind: the opening into the mastoid cells. On the outer wall: the opening for the membrana tympani, the *iter chordæ anterioris*, *iter chordæ posterioris*, and the *Glaserian fissure*. On the inner wall: the *fenestra ovalis*, *fenestra rotunda*, and an opening on the apex of the pyramid for the stapedius muscle. The other objects which demand attention are: the *pyramid* from the apex of which the stapedius muscle emerges, the *promontory* (*tuber cochleæ*) on the inner wall, formed by the first turn of the cochlea, and the ridge on the same wall formed by the *aqueductus Fallopii*. Of the fenestræ the oval one which opens into the vestibule is larger in size, and placed above the other. The round opening leads into the cochlea, and is closed in by the *membrana tympani secundaria* (of Scarpa).

Of the parts of the internal ear or labyrinth, the cochlea is placed most anteriorly, the vestibule intermediate in position, and the semicircular canals behind. The latter are three in number, of which the external is horizontally placed, while the planes of the other two are vertical. Each forms about two-thirds of a circle; they open into the posterior wall of the vestibule, and as the posterior and superior coalesce behind, there are but five openings. The diameter of each canal is about $\frac{1}{8}$ th of an inch, and each holds in its interior a membranous tube of about one-third its breadth, and adherent to its periosteal lining along the convexity. Surrounding the membranous canal in the *perilymph* (*liquor Cotunnii*); within it is the *endolymph* (*liquor Scarpæ*). The wall is formed of three layers: an external (*fibrous*), which adheres to the periosteum; a middle (*tunica propria*), of hyaline aspect, and raised on the inner side (except opposite the adhering part) into papilliform elevations; and an internal, formed by a single layer of tessellated epithelial cells. Towards the end, each canal swells out to form the *ampulla*, which nearly fills the corresponding ampulla of the osseous tube. Here the epithelium is of the columnar variety, and an elevation on the side next the bone forming the so-called *crista ampullæ*, which partly divides the cavity into two compartments. On this crest the epithelial cells are of an elongated columnar shape, between which are placed slender spindle-shaped cells, which send stiff

hair-like processes (*auditory hairs*) to project into the endolymph. The other end of each of these cells sends a process downwards, to communicate with the branched ending of a nerve-fibre.

The *vestibule*, or central chamber of the labyrinth, is irregularly ovoid in shape, with the longer axis from before backwards. The cavity is somewhat compressed from within outwards. The former axis is about $\frac{3}{4}$ th of an inch, the latter is a little less.

On the outer wall is the *fenestra ovalis* (already mentioned) which communicates with the tympanic cavity. On the inner wall are placed from before backwards: the *fovea hemispherica*, which corresponds to the macula cribrosa, and is perforated by small holes for branches of the auditory nerve, coming from the internal meatus. This fossa is limited behind by the *crista vestibuli* (*eminentia pyramidalis*) which separates it from the *aqueductus vestibuli*, a small canal conveying a vein to the posterior surface of the temporal bone. In the roof is another fossa, of transversely oval shape, the *fovea hemi-elliptica*; in front is the *apertura scalæ vestibuli*, and behind are the five openings of the semicircular canals.

Within the *osseous* is the *membranous vestibule*, which consists of two connected sacs, and the tubes by which they communicate with the membranous semicircular canals and cochlea. Of these two sacs, the larger is the *utricle* (common sinus) which lies in the upper and back part of the cavity, occupying the fovea hemi-elliptica. Minute crystalline masses of carbonate of lime are attached to its walls (*otoliths, otoconia*). The posterior part receives all the openings of the semicircular canals. The other membranous bag, the *sacculæ*, is more spherical in shape, and is placed in the anterior part of the osseous cavity occupying the fovea hemispherica. It also contains otoconia in its wall.

The sacculæ is connected with the *canalis membranaceus* of the cochlea, by means of the *canalis reuniens* of Hensen, and the two cavities (utricle and sacculæ) communicate by means of a Y-shaped canal, of which the stalk occupies the *aqueductus vestibuli*, while it sends a branch to either cavity.

The *cochlea* is of a somewhat bluntly conical shape, with the base directed inwards. The length of the axis is about $\frac{1}{4}$ th of an inch, and the breadth of the base is about the same. A bony central column (*modiolus*) forms an axis around which

turns the *lamina spiralis*, so as to give the cavity the appearance of a coiled tube making two and a-half turns. The inner part (*lamina spiralis ossea*) projects half way across the cavity at the base of the cochlea, and, from the free margin, the *lamina spiralis membranacea* passes across to the opposite wall of the cavity, dividing the latter into two passages *scala vestibuli* (above), and *scala tympani* (below) which communicate, at the apex of the modiolus, by an opening called the *helicotrema*. Each is about $2\frac{1}{2}$ inches long, and the turns are from left to right in the right ear, and in the opposite direction in the left.

The communication at the apex presents the arched extremity called the cupola.

The *modiolus* (*columella*) is perforated in the centre by the *canalis centralis modiolii* for the passage of vessels and nerves from the base to the apex. Winding around this axis is the *canalis spiralis modiolii* (Rosenthal), placed close to the *lamina spiralis*. The *canalis ganglionaris* of Rosenthal lodges the ganglion spirale of the auditory nerve. The *lamina spiralis ossea* passes half way across the cavity at the base of the cochlea, but it diminishes in width as it passes towards the apex, while the membranous lamina becomes proportionally wider. It terminates at the apex in a hooked process the *hamulus*.

The *scala tympani* commences at the fenestra rotunda, and receives near its commencement, the *aqueductus cochleæ* which transmits a small vein. The *scala vestibuli*, which is above, is somewhat narrower than the other at the commencement.

The *membranous labyrinth* presents great complexity of structure. From the outer end of the *lamina spiralis ossea* stretches the *membrana basilaris* straight across, to join the lining periosteum, by means of the *ligamentum spirale* (*cochlearis muscle* of Todd and Bowman). At a little distance from the free margin of the osseous spiral lamina the *membrane of Reissner* is observed to arise, and proceed obliquely upwards and outwards to the periosteum. The triangular canal placed between this and the basilar membrane is called the *ductus cochlearis* (*canalis membranaceus cochleæ*). This terminates at each end in a pointed extremity, and the end next the base communicates with the saccule by means of the *canalis reuniens*.

At the free margin of the osseous spiral lamina is the thickened periosteal ridge called the *limbus laminae spiralis* (*denticulate lamina* of Todd and Bowman), which overhangs the C-shaped recess called the *sulcus spiralis*. The upper margin of the C forms the *labium vestibulare* of Henle; the lower, the *labium tympanicum*. Passing outwards from the margin of the osseous spiral lamina is the *membrana tectoria* (Claudius), between which and the basilar membrane is placed the *organ of Corti*. This very peculiar structure is formed of two rows of peculiarly modified cells, resting by one end on the basilar membrane, while the other ends meet like the rafters of a house. The space beneath is called the *tunnel of Corti*. The inner cells are each shaped somewhat like the human ulna, while the outer have been compared to the head, neck, and bill of a swan. At the foot of each is a protoplasmic mass enclosing a nucleus. On each side of Corti's cells are placed *hair-cells*; one row to the inner side of the inner cells, and three or four to the outer side of the others. The hair-like processes pass through openings above, which are bounded by minute rings (Böttcher), and fiddle-shaped structures called phalanges (Deiters). These form the *lamina reticularis* of Kölliker, which covers the organ of Corti like a wire net, beneath the *membrana tectoria*. Outside the outer rods of Corti is the longitudinal arteriole, called the *vas spirale*. Between Reissner's membrane and the ligamentum spirale is the *ligamentum spirale accessorium*, formed by a small periosteal elevation. Above this is the vascular portion of the periosteal lining known as the *stria vascularis*.

The inside of the scalæ is lined by a layer of endothelial cells, while that of the ductus cochlearis presents flattened epithelium.

Vessels and nerves.—The cochlea branches (12—14) of the *auditory artery* lie in the small canals of the modiolus, communicating at intervals with the *vas spirale*. They form in their ascent towards the apex a fine plexus, from which branches pass along the periosteum in all directions. The veins pass chiefly to the superior petrosal sinus.

The *cochlear branch* of the *auditory nerve*, after entering through the macula cribrosa, passes from the furrow at the base of the cochlea (*tractus spiralis foraminulentus*) into the canals of the modiolus. In one of these canals, as already mentioned,

lies the *ganglion spirale*, through which the nerve-fibres pass, each having probably a ganglion-cell interposed in its course. From this structure the fibres pass towards the edge of the osseous spiral lamina, and at its margin are supposed to communicate with the cells of the organ of Corti.

Transmission of sound.—(1) *In the external ear.*—The vibrations of sound are transmitted to the auricle, from which many are reflected back to the external ear, while a certain portion undergo a series of reflections which direct them into the external auditory canal. The greater part of those which impinge upon the concha are reflected to the inner surface of the tragus from which they are directed into the meatus; the concha in this way fulfils a function analogous to that of a concave mirror. The irregularity of the surface of the pinna enables us to judge more correctly of the direction and the intensity of the sound, as according to the direction, a larger or smaller proportion of the waves of sound are collected, and the inequalities direct the waves of sound towards the concha. If these inequalities are obliterated by filling them smoothly over with wax, while the meatus is left free, the intensity of the sounds is diminished, and it becomes more difficult to judge of their direction (Schneider).

In the external meatus the waves of sound undergo a series of reflections which conduct them to the membrana tympani. On account of the obliquity and curves of that membrane, most of these waves strike it in a nearly perpendicular direction. A portion of the waves are reflected back to the outer air, and this reflection is the more powerful, as the membrane is more tense, and more obliquely placed.

(2) *In the middle ear.*—The tympanic membrane is thrown into vibration by the waves in the external meatus. These vibrations have been demonstrated by Mach and Kessel with the aid of a special apparatus, and also by the stroboscopic method. They are transmitted to the ossicles, and the movements of the latter have been registered by Politzer in pathological cases. The vibrations of the membrane are produced for all sounds in the interval of perceptible sounds, and in such respect this differs from ordinary membranes, which are thrown into vibration only by a sound corresponding to their proper sound, or one of its multiples. In general terms it enters into vibration more easily for acute sounds than for grave, but the

most important influences are :—(a) the anatomical disposition, and (b) the differences of tension.

The attachment of the handle of the malleus to the membrane diminishes the vibrations of the latter, especially as the vibrations approach those proper to the membrane. It also lessens the consecutive vibrations, which without this influence would have the effect of prolonging the sound.

The tension of the tympanic membrane is influenced by two causes : (a) the relative *pressures of the air* on its external and internal surfaces (this cause acts but occasionally, as in forced expirations, &c.) ; (b) *muscular action*.

The *tensor tympani* usually contracts involuntarily and by reflex influence, except in connection with energetic contraction of the muscles of mastication, of which it forms an accessory phenomenon. This is accompanied by a crepitating noise, attributed by some to sudden tension of the tympanic membrane ; by others, to sudden opening of the Eustachian tube, by the simultaneous contraction of the tensor palati.

The *laxator tympani* can hardly have any important physiological influence. The action of the *stapedius* is still imperfectly understood. According to Pollitzer it is antagonistic to that of the tensor tympani muscle, and Lucae believes that it is thrown into action during elevated (*non-musical*) sounds.

The variations of tension of the membrane act in two ways : (1) It forms a true apparatus of accommodation ; it is made tense during acute sounds, while it is relaxed during the more grave, so as to modify the proper sound of the membrane ; (2) It muffles sounds by increase of tension, and diminishing the intensity of the vibrations, especially for grave sounds.

The vibrations of the *membrana tympani* are transmitted to the fluids of the labyrinth in two ways : (1) by the air of the cavity ; and (2) along the *ossicula auditus*. The first is the less important ; by it the vibrations are transmitted to the *fenestra rotunda*, and so to the cochlea. The other line of communication is more important. The vibrations transmitted from without cause a transverse movement of the bones. The articulations of the latter, and their investment of mucous membrane, diminish the facility of the transmission of vibrations in the interior of the chain of ossicles, without preventing their vibration as a whole.

(3) *In the internal ear*.—The auditory vibrations arrive at

the fluids of the labyrinth in three ways: (*a*) by the osseous walls of the labyrinth; (*b*) by the air of the tympanum and the fenestra rotunda; (*c*) by the stapes and fenestra ovalis, which is the most important.

(*a*) The transmission by the bones takes place in a certain class of cases, as when a vibrating body (watch, tuning fork, &c.), is placed between the teeth. It is by this means that we hear our own voices; the vibrations of the air in the mouth and nasal fossæ are transmitted to the walls of the cranium; so that the line of conduction is then the reverse of what we have in the ordinary conditions, and a certain part of the vibrations is lost by the external auditory canal, so that, if the ears are closed, one's own voice is more distinctly heard.

(*b*) Pollitzer has shown experimentally, by adjusting a small manometer to the labyrinth, that the variations of pressure of the air in the external meatus, and in the tympanum, cause corresponding variations of pressure in the labyrinth. Accordingly, these vibrations pass through the fenestra rotunda, but this mode of transmission is of comparatively little importance.

(*c*) The movements of the ossicles are transmitted from the base of the stapes at the fenestra ovalis to the labyrinthine fluids, and the alternate yielding of the secondary tympanic membrane can be seen directly on the dead body. These oscillations are transmitted to the auditory nerve-endings.

In the cochlea, the vibrations pass, from base to summit along the scala vestibuli, and from apex to base along the scala tympani. From the latter they are reflected in the opposite direction, and as a constant succession of waves and reflections in this direction occur, stationary vibrations result, like those of a cord fixed at both ends, and, consequently, similar vibrations in the scala media, which contains the organ of Corti and the terminations of the cochlear nerves.

Besides affecting the cochlear fluids the piston-like strokes of the stapes are transmitted to the fluids of the semicircular canals. The exact use of these tubes, however, remains purely hypothetical.

Auditory sensations.—The conditions necessary for the production of an auditory sensation are: (*a*) that the vibrations are of sufficient strength; (*b*) that they have a certain duration; above or below a certain number of vibrations per second, sounds cease to be perceptible. The limits vary in

different individuals, but, for the most part, they lie between the inferior extreme of 80 vibrations per second to the superior one of 20,000. The extreme limits are 16—40,960 according to Preyer.

Auditory sensations are of two classes: *musical sounds* and *noises*. Physically, a musical sound corresponds to periodic and regular vibrations, a noise to irregular and non-periodic, or to instantaneous shocks. Physiologically, the sensation of a musical sound is a simple sensation of regular nature, while that of a noise is complex and irregular. But as noises are, when analysed, found to be the resultant of a number of musical sounds irregularly mingled, we need occupy ourselves only with the consideration of the latter.

Physical characters of auditory sensations.—These are three in number: intensity, height, and timbre.

(a) *Intensity of sound.*—The intensity depends on the *amplitude* of the vibrations. There is hardly any fixed measure of the intensity of sounds, and the appreciation is only relative, and varies greatly in different persons. We are usually able to appreciate a difference of 72—100 in the intensity of a sound. Schafhäütl has found the inferior limit of auditory sensation to be the sound produced by one milligramme of lead falling from a height of one millimetre.

For the purpose of increasing the acuteness of hearing many kinds of apparatus have been employed: tuning-forks (Conta, Magnus), metallic wires (Politzer), vibrating rods (Blake), &c. The most perfect are the audiometer of Hughes, and the interauricular tube of Gellé.

(b) *Height of sound.*—This depends upon the number of vibrations. The height of a sound is estimated, not absolutely, but relatively to another sound. A sound is more grave than another, when it causes a less number of vibrations per second; more acute, when it causes a greater number. Beyond certain limits, the appreciation for higher sounds ceases to exist. There are: for grave sounds, 33 vibrations per second; for acute sounds, 4,500. There is a great difference in individuals between the powers of appreciating the height of sounds; a musical ear distinguishes clearly a difference of $\frac{1}{300}$ th (some can appreciate a difference of $\frac{1}{1000}$ th).

(c) *Timbre of sound.*—The timbre depends, as we have already seen, on the number and intensity of the harmonics of

the fundamental sound. These partial harmonics accompany nearly all musical sounds, but, habitually, they escape notice as distinct auditory sensations, and are joined in one sensation, which is attributed to the fundamental sound. They can be separated, however, by careful attention and by the aid of special instruments (resonators). Among the harmonics we distinguish more easily the partial odd sounds (fifth, third, &c.) than the even ones.

Physiological characters of auditory sensations—One of the most essential of these is the sensation of *exteriority*, by which sounds are referred to the outer world. It appears to be produced outside our bodies, and we judge of the distance by its intensity, and of the direction by the position of the external auditory canal. This sensation appears to be due to the vibrations of the tympanic membrane, for, when the head is under water all sounds are referred to the interior of the head. Habitue also probably influences it.

The *duration* of an auditory sensation surpasses that of the sonorous vibration which gave rise to it. We are able to distinguish 133 strokes per second, but beyond this number the sensation becomes continuous, because the impressions become fused together (Helmholtz). In certain cases the effect on the auditory nerves lasts a considerable time, so as to give rise to *consecutive auditory sensations*.

The *sensibility* of the ear for sounds of different heights is not uniform; it is usually more vivid for acute sounds than for grave; the maximum sensibility of the ear is for the numbers of vibrations ranging between 2,800 and 3,000. It varies much in different individuals; musicians recognise differences of height of $\frac{1}{16}$ of a semitone, whereas untrained ears are scarcely affected by a semitone; this delicacy of appreciation constitutes the *justness* of the ear.

This sensibility of the ear judges not only of the height, but also of the intensity and timbre of sounds. By the timbre of a sound, we recognise at once the instrument which produces it; we know an acquaintance by the timbre of his voice.

Exercise and *habitude* may bring this sensibility to a high degree of perfection.

Auditory sensations sometimes furnish the stimuli to reflex movements (laughing, tears, muscular contractions, &c.); indeed, they rank in this respect next to tactile sensations.

The mode of stimulation of the nervous structures is very imperfectly understood. We only know that some mechanical agitation takes place, but we are uncertain how this vibration is able to produce the different kinds of auditory sensations. The hypothesis of Helmholtz is, at least, very ingenious, and has been accepted by many. He supposes that the elastic arches (about 3,000 in number), formed by the cells of Corti, correspond each to a certain sound, and so form a regular series, which corresponds to the scale of the gamut. 2,800 of these arches would then correspond to the musical sounds, properly so-called, which makes up seven octaves; this would make 400 fibres for an octave (nearly 33 for a semi-tone). The experiments of Hensen go to confirm the hypothesis of Helmholtz; the mysis (crustaceæ), present external auditory hairs, and this observer, by producing musical sounds in the water, has seen certain hairs vibrate for particular sounds, and other hairs for the different ones.

It would seem that the admission of 33 fibres of Corti for the sound comprised in the interval of a semi-tone would be insufficient, for we can easily distinguish a difference of height of $\frac{1}{4}$ th of a semi-tone, but this may be explained by the suggestion, that an intervening sound causes a vibration of the two adjacent arches.

Recent researches have, however, thrown great doubt on this hypothesis. The organ of Corti is wanting in birds, who undoubtedly, appreciate the height of sounds. This observation has led Helmholtz to transfer the function to the *membrana basilaris*; which forms, according to him, a series of parallel cords, increasing in length from the apex to the base of the cochlea, and arranged each for a certain sound.

The *utricle* and *sacculæ* appear to be connected with the sensations of shock; the cochlea with those of height and timbre.

Hearing with two ears: binaural audition.—The hearing of a single sound with both ears may be due to habit, or to the connection in the nerve-centres of the fibres connected with both ears, but the question cannot be settled by our present means of investigation. There is no doubt that binaural audition facilitates our knowledge of the direction of sound; each ear having its own auditory axis and direction.

Simultaneous auditory sensations.—A very great number of simultaneous auditory sensations can be distinctly appreciated;

and, indeed, it is hardly possible to say what limit there may be to the number. If the time separating two auditory sensations be very short they may appear simultaneous, but an interval of $\frac{1}{12}$ sec. is sufficient to give distinct sensations of two sounds. In the simultaneous audition of various sounds we must distinguish between the case in which they reach both ears, or but a single one. If two sounds simultaneously produced have the same height, the same intensity, and the same timbre, they have the effect of a single sound, whether heard by one ear, or both. If they differ in height and timbre, both are distinctly heard with the two ears; with a single ear, on the other hand, they give but a single sensation, a sound resulting from the composition of the two primitive ones.

SIGHT.

The eye, or organ of vision, is a structure of extreme delicacy as well as complexity, and requires for its protection the shelter of the bony walls of the *orbit* in which it is placed, as well as the additional safeguards afforded by the eye-lids, lachrymal apparatus, &c. These protective structures are collectively called the *tutamina oculi*.

The eye-lids (*palpebræ*) are muco-cutaneous flaps, strengthened towards their margins by a thin lamina of dense connective tissue (*tarsal cartilage*), and containing a layer of muscular tissue, the *orbicularis palpebrarum* (*sphincter oculi*). The opening between the eye-lids (*fissura palpebrarum*), exposes the anterior portion of the eye-ball for transmission of light. The angles of the fissure are called *canthi*. Near the inner canthus is an elevation on either eye-lid (*papilla lachrymalis*), the apex of which is pierced by the *punctum lachrymale*, which forms the mouth of the *canaliculus lachrymalis*. The mucous lining of the lids is called the conjunctiva. The part which covers the back of the eye-lid is called the *palpebral*, and that which is reflected over the anterior surface of the eye-ball is called the *ocular*, conjunctiva. The angle of reflection is the *fornix* (*retro-tarsal fold*) of the conjunctiva. The angular recess formed by the fornix is called the *palpebral sinus*. At the inner canthus a group of sebaceous glands, which open into the follicles of very fine hairs form the elevation called the *caruncula lachrymalis*, beside which the conjunctiva forms the vertica-

fold (*plica semilunaris*) which represents the *membrana nictitans* of birds. It contains some smooth muscle cells. On the margins of the lids open the ducts of the *Meibomian glands*, of which there are from twenty to thirty for each lid. They form nearly straight tubes, with numerous coecal appendages along the sides, and are placed immediately beneath the ocular conjunctiva. They are lined by cubical epithelium, and secrete an oily fluid which prevents the adhesion of the palpebral margins.

The palpebral conjunctiva is thick, reddish, and vascular, and presents numerous delicate papillæ, freely supplied with nerves. A layer of small racemose glands is found beneath it, the ducts of which open near the fornix (Sappey, W. Krause). With the aid of a lens, numerous small folds may be observed in the membrane.

The *ocular conjunctiva* is thinner than the palpebral, and more loosely connected to the subjacent structures. It has fewer blood-vessels; is transparent in structure, and deficient in papillæ.

The conjunctival epithelium is mainly columnar. The corneal conjunctiva consists of epithelium alone, the structure of which shall be again referred to.

The *lymphatics* do not present any special peculiarity. The back part of the conjunctiva presents a good deal of lymphoid tissue. The *nerves* seem to be arranged similarly to those of the skin, and according to Krause, many of them terminate in end-bulbs.

Lachrymal apparatus.—The tear-gland is placed in the *fossa lachrymalis*, at the upper and outer angle of the orbit, where it adheres to the periosteum by fibrous bands. There are two lobes, the antero-inferior one (*glandula lachrymalis inferior* of Rosenmüller) being the smaller. The ducts from both, 12—14 in number, are short and straight, and open on the conjunctival surface at the outer part of the fornix superior. The tears which are transmitted from these ducts to the conjunctival surface pass into the puncta, after being washed over the front of the eye-ball by the contraction of the orbicularis palpebrarum.

The canaliculi proceed vertically from these openings, the upper at first ascending, and the lower descending; each then makes a sudden angular bend, from which they converge to join the lachrymal sac, sometimes by a common mouth, but more often separately. The upper canal is somewhat the longer and

narrower, and each presents a dilatation at the bent portion. From the lachrymal sac, the nasal duct passes downwards, with a slight obliquity backwards and outwards (*inwards* according to Krause) to open into the anterior part of the inferior meatus. At its termination a fold of mucous membrane (valve of *Hasner*) prevents regurgitation. Another small fold (*valve of Huschke*) is placed at the opening of either canaliculus into the lachrymal sac. In this situation Rosenmüller found a small valve above the common opening (*valvula sacci lachrymalis, plica Rosenmülleri*): Arnold discovered one immediately below the opening. This latter corresponds to the *valvula sacci lachrymalis superior* of Béraud, which, according to Foltz and Bochdalek presents in the middle of its free margin a nodule of fibrous tissue, analogous to one of the corpora Arantii in the sigmoid valves at the mouth of the aorta. At the origin of the lachrymal canal from the sac, is the *valvula sacci lachrymalis inferior* of Béraud. Another fold of mucous membrane (*valve of Foltz*) is placed close to the punctum lachrymale in the first part of the canaliculus.

The eye-ball.—The globe of the eye (*bulbus oculi*) is nearly globular in shape, with a small segment of a smaller sphere, placed in front. It may be said to be formed by three coats, enclosing certain transparent structures. The external (*fibrous*) coat is formed by the *sclerotic* and *cornea*, the middle (*vascular*) comprises the *choroid*, *ciliary processes*, and *iris*; the internal (*nervous*) includes the *retina* only.

The eye-ball is moved by six muscles: four *straight* and two *oblique*, and its movements are facilitated by a smooth investing membrane, *tunica vaginalis oculi* (*capsule of Tenon, O'Ferrall's ocular fascia*), which is formed of two layers lined by endothelial cells and enclosing a lymph-space.

The antero-posterior diameter of the globe of the eye is about $\frac{1}{8}$ th of an inch; the transverse diameter exceeds this by about a line on account of the antero-posterior compression of the eye-ball. Without this flattening, the antero-posterior axis should be the longer, from the projection of the cornea in front.

Sclerotic.—This tunic (*cornea opaca*) is formed of fibrous lamellæ, the bundles of the successive layers crossing one another so as to give the greatest possible strength. Fine elastic fibres are found among the others, and, in the interspaces, connective-tissue corpuscles are placed. It is thickest behind in the neigh-

bourhood of the part pierced by the optic nerve (*lamina cribrosa*) which is placed about a tenth of an inch inside the antero-posterior axis. Here the *dura-matral* sheath of the nerve blends with the sclerotic, which is also strengthened in front by an expansion (*tunica albuginea oculi*), derived from the tendons of the ocular muscles. The sclerotic thins a little as it passes forward, and is weakest about two lines from the cornea; the anterior portion again increases in thickness.

The *cornea* (*cornea pellucida*). This clear portion of the tunic of the eye-ball forms a segment of a sphere, of smaller curve than that of the sclerotic. It extends to about one-sixth of the circumference. It is joined to the sclerotic coat by direct continuity of tissue, and its anterior surface is overlapped a little, so as to make this a little smaller than the posterior surface. This overlapping has suggested the well-known simile of the setting of a *watch-glass*. The layers which make up the structure of the cornea are as follows: (1) an *epithelium*, derived from the conjunctiva, of which the superficial cells are flattened, while the deeper cells are round or polyhedral in shape, with a single layer of columnar cells beneath. The *fingered cells of Cleland* are some of the polyhedral, which send processes between those below them. (2) The *anterior elastic lamina* (Bowman) is formed by the superficial part of the proper structure of the cornea, which is denser than the rest of the tissue, and free from corpuscles. Its depth is $\frac{1}{8000}$ — $\frac{1}{7000}$ th of an inch, but it cannot be easily separated, as curved fibres pass between it and the corneal tissue proper. (3) The *corneal propria* is formed of delicate lamellæ of fibrous tissue (about 60 in number), the bundles of which cross those of adjacent layers at right angles. Between the lamellæ are the cell-spaces, which communicate by minute channels (*Recklinghausen's canals*), and hold the stellate *corneal corpuscles*, which send processes along these canals. In vertical sections these corpuscles appear fusiform; in transverse sections flattened; while around them and their processes sufficient space is left for the nutrient plasma to trickle along, for the nutrition of the surrounding tissue. (4) The *posterior elastic lamina* (Bowman), *membrane of Demours* (or of *Descemet*). This lamina is $\frac{1}{8000}$ — $\frac{1}{7000}$ th of an inch in thickness, firm and homogeneous in structure, and more easily separated than the anterior, although thinner. Separated pieces tend to curl up, with their attached surface innermost. At the circumference, this lamina

breaks up into bundles of fibres, some of which form the pillars of the iris, while others pass into the sclerotic and choroid coats. (5) The *epithelium* of the anterior chamber, which is formed of a single layer of flattened polygonal cells.

The epithelium is deficient at the circumference in the intervals between the pillars of the iris. The openings so formed are the mouths of cavernous spaces (*spaces of Fontana*) which lead into the circumferential channel (*sinus circularis iridis*, or *canal of Schlemm*), through the intervention of which the anterior chamber is placed in communication with the veins of the sclerotic coat (*Schwalbe*).

Blood-vessels or *lymphatics* are not traceable in the cornea in the normal state. The *nerves* are very numerous. They form *primary plexuses* in the substance of the cornea, from which more delicate branches proceed to *sub-epithelial* and *inter-epithelial plexuses*, the latter of which extends nearly to the free surface.

The inner surface of the sclerotic is of a light brown color, and joined by a layer of connective tissue to the subjacent tunica choroidea. This layer is subdivided by a lymph space into two laminæ: the *membrana fusca*, which adheres to the sclerotic, and the thinner *lamina supra-choroidea*. Grooves for the ciliary vessels and nerves are also found on the deep surface.

The *choroid* is chiefly formed of blood-vessels. The arteries, as already mentioned, groove the sclerotic coat before passing into the choroid. After passing into its substance they get beneath the veins, while the latter (*vasa vorticea*) receive their tributaries as curved branches, arranged in a peculiar form, which has been compared to the branching of a weeping willow, and form four or five large trunks, which pierce the sclerotic, half way between the entrance of the optic nerve and the margin of the cornea. The inner part of the choroid coat is formed by the capillary blood-vessels (*tunica Ruysschiana* vel *chorio-capillaris*). This reaches to $\frac{1}{16}$ th of an inch from the corneal margin, where its vessels join those of the ciliary processes. This layer is separated by a delicate homogeneous lamina (*membrane of Bruch*) from the pigmentary layer of the retina beneath.

The ciliary body comprises the ciliary processes, and ciliary muscles.

The *ciliary processes*, about 70 in number, are formed by bulbous masses of coarse capillaries. They are of unequal length, about one-third of the number being long, and two-thirds short.

Ciliary muscle (Bowman) tensor choroides.—This forms a rim of unstriped muscle cells, attached by a tendon to the sclerotic close to the cornea, from which it radiates to be inserted into the tissue of the choroid coat. The anterior fibres, at the margin of the iris, pass into a ring of smooth cells, the *ciliary ligament* of Bowman, more correctly described by H. Müller as a *circular ciliary muscle (compressor lentis)*.

Iris.—The iris, the color of which characterises the eye of each individual, is so called from the various tints it presents in different persons. The central aperture for the transmission of light is called the *pupil*, the diameter of which may vary in the normal state from $\frac{1}{16}$ th— $\frac{1}{3}$ rd of an inch. It is placed a little to the inner side of the centre of the iris.

The circumference is connected with the ciliary body and the adjacent margins of sclerotic and cornea. At its edge Descemet's membrane also sends fibres to blend with it; these form the *pillars of the iris (ligamentum pectinatum iridis)* of Hueck).

The tissue of the iris includes smooth muscle cells, with a copious supply of blood-vessels and nerves. Its anterior surface is covered by a layer of flattened epithelial cells continued from the back of the cornea, while the posterior surface presents a layer of pigment cells prolonged from those of the retina, from the peculiar tint of which this layer is called the *uvea*. The muscular fibres are *circular* and *radiating*. The former are arranged as a narrow zone ($\frac{1}{16}$ th of an inch in breadth) around the margin of the pupil, *sphincter pupillæ*, (*sphincter iridis* of Cloquet). They are behind the radiating fibres, which are much more numerous. The former are supplied by the third nerve: the latter by the sympathetic.

A variable amount of *pigment cells* are scattered through the substance of the iris, and to their proportion is due the color of the latter.

The vascular supply is chiefly from the long ciliary arteries. By the branches into which the two divide a vascular ring (*circulus major*) is formed, which lies in the canal of Fontana, and from the branches of which a smaller anastomotic circle (*circulus minor*) is formed in front of the other.

Retina.—The thickness of the nervous coat of the eye diminishes from behind forwards ($\frac{1}{80}$ th to $\frac{1}{160}$ th of an inch). In the fresh eye it is transparent, and of a light pink color. It reaches forwards as far as the ciliary processes, where it terminates in a

wavy border, the *ora serrata*. The layers of this coat, as described by Max Schultze are as follow (in order from within outwards) :

1. Membrana limitans interna.
2. Nerve fibres.
3. Nerve cells (ganglionic layer).
4. Inner molecular.
5. Inner nuclear.
6. Outer molecular.
7. Outer nuclear.
8. Membrana limitans externa.
9. Rods and cones.
10. Layer of pigment cells.

These layers are united by the radial *fibres of Müller*, which pass between the limiting membranes.

(1). This is a homogeneous membrane placed in contact with the hyaloid membrane of the vitreous humor.

(2). This layer is derived from the fibres of the optic nerve with which it is directly continuous. The fibres have no primitive sheath, and in the retina the medullary sheath disappears, so that they are here formed of axis-cylinders only. Each is probably connected with an axis-cylinder process of the cells of the next layer.

(3). The cells of this layer are pyriform in shape, from one end of which each sends an unbranched axis-cylinder process among the fibres of the last-mentioned layer, with one of which it is, doubtless, continuous. A larger branching process passes into the next layer.

(4). *Inner molecular (granular layer)*.—This is chiefly formed by a delicate fibrillar meshwork. It is thicker than the outer molecular layer, and like the latter its function is that of a supporting structure. The branching processes of the ganglion cells pass into it (this is denied by some), and also the processes from the bipolar cells of the next layer.

(5). *Inner nuclear layer*.—Three kinds of cells are found in this layer. (1) A layer of flattened cells with anastomosing branches placed parallel to the surface ; (2) elongated spindle-shaped cells with very large nuclei, and placed with the long axis perpendicular to the surface. One process passes into the layer last described ; the other passes into the outer molecular, and communicates either with the rods or cones of the bacillar

layer. According to Merkel, the rod-processes are branched but not the cone-processes; this distinction is denied by Kuhnt, according to whom both are branched. The cells of this layer have hardly any distinct limiting membrane. (3) This layer presents long oval nuclei, connected with Müller's fibres, in the course of which they lie.

(6). *Outer molecular (granular) layer*.—This is formed by a dense meshwork of delicate fibrils, presenting minute varicosities, and imbedded in a homogeneous matrix. It is penetrated by Müller's fibres, and according to most observers, the latter send small lateral fibrils to the network.

(7). *Outer nuclear layer*.—The nuclei of this layer are placed, one on each of a series of fibrillar prolongations from the bases of the rods and cones of Jacob's membrane, *rod-fibres* and *cone-fibres*. They are imbedded in a homogenous matrix, which also contains an independent fibrillar network.

(8). *Membrana limitans externa*.—Seen from the surface this appears as a reticular membrane perforated for the passage of the ends of the rods and cones.

(9). *Rods and cones. Membrana Jacobi. Bacillar layer*.—This layer can, in a perfectly fresh eye, be separated as a distinct membrane by careful dissection. This may be done under water, which was the mode of demonstration employed by its discoverer, the late Dr. Arthur Jacob, of Dublin.

Two distinct characteristic structures are found in this layer, the rods and cones. Each *rod* consists of an outer and inner portion. Continued strong light causes swelling of the rods, but they shrink again in darkness (Ewald, Kühne). The outer portion differs in refracting power, &c., from the inner; it has a cylindrical shape, and bright glistening appearance. The outer portion of both rods and cones is, according to Kuhnt, made up of neurokeratin. A dilute solution of potash separates the outer rod-segments into transverse plates (*Hannover's discs*). According to some observers, a central thread-like axis appears in each after treatment with dilute chromic acid (*Ritter's filament*).

The inner member is of the same length as the outer, and presents convex surfaces. It is joined to the outer by a thin layer of cementing substance. It shows a faint longitudinal striation, due to the presence of fine fibrils prolonged on its outer surface from the *limitans externa* (Krause, Max Schultze).

Fine bright fibrils are found in the cortical portion of each (Max Schultze); and an axial thread-like filament is also present (Krause).

Each *cone* is also formed of an inner and outer segment. The outer is short and conical; the inner broader, and with convex sides. The former, like the outer rod-segment, easily separates into transverse discs, while the inner portion presents the longitudinal fibrillar sheath prolonged from the *limitans externa*. The cortical portion of this segment of the cones is also longitudinally striated.

In man and most mammals the number of rods far exceeds that of the cones; the reverse is the case in birds.

(10). *Pigmentary layer*.—The hexagonal pigment cells of the outermost layer of the retina were referred to the choroid, before Max Schultze's investigation of its development led to a more correct view. Seen in vertical section, these cells present numbers of pigmented rods, which contain rhomboid flattened crystals with sharp angles (Frisch). The part of the cell next the choroid coat is free of pigment, and contains a flattened nucleus, placed parallel to the surface.

Macula lutea.—The yellow spot of Sömmering is an oval depression in the centre of the retina, $\frac{1}{16}$ th of an inch across. Its centre is the *fovea centralis*.

Crystalline lens.—This is a biconvex lens enclosed in an elastic capsule, which is thicker in front than behind, the thinnest part being at the posterior pole. The anterior part of the capsule is lined by epithelial cells, the liquefaction of which after death is the source of the so-called *liquor Morgagni*.

The lens is biconvex; the greater convexity being on the posterior surface. The transverse and vertical diameters are about $\frac{1}{3}$ rd of an inch, and the antero-posterior $\frac{1}{4}$ th. On both surfaces are faint white lines radiating from the centre, dividing it into three sectors of equal size. On the anterior surface they are arranged in the form of a Y; on the posterior surface they form the same letter inverted. These lines correspond to the planes of ending of the lens fibres.

The substance of the lens is made up of the lens fibres (originally epithelial cells) arranging in concentric layers, traceable from the posterior surface to the anterior. Each contains a nucleus, indistinct in the deeper parts of the lens, but quite plain near the margins, where they form the *nuclear zone* of *Mayer*.

The shape of each fibre is that of a hexagonal prismatic band. The interior presents longitudinal striations, and the surfaces are covered with ridges and furrows which dovetail with those of adjacent fibres. The whole is cemented by an albuminous interstitial substance, in which canals are found for the passage of the nutritive fluids.

Aqueous humor.—This fluid contains about 2 per cent. of solids, chiefly chloride of sodium. It occupies the *anterior chamber*, or space between the back of the cornea and front of iris (and pupil). The so-called *posterior chamber* (between back of iris and front of lens) can hardly be said to exist as a space.

Vitreous humor.—This body is enclosed in a homogeneous capsule, the hyaloid membrane, which passes in front to the margin of the lens as the *zonula of Zinn* (s. *ciliaris*), which is the strongest part, and forms the anterior wall of the lymph-space usually known as the *canal of Petit*. According to others, it splits to enclose this space.

On the inner surface of the hyaloid are small granular cells, the *sub-hyaloid cells of Ciaccio*, possessing amoeboid movements.

The substance of the vitreous body appears to be arranged in laminæ; concentric on the outside, radiating in the deeper parts.

In the centre is the *canal of Stilling* (or of Cloquet) which in foetal life transmitted the *artery of Zinn* to the back of the lens-capsule. The remains of a few other vessels are found here and there as solid fibres (Lieberkühn).

Sight or vision (*visual sensation*) is the special sensation resulting from stimulation of the retina by light. In addition to the existence of the stimulus (light) and the sensory surface (retina) the following parts are necessary to complete the apparatus required for perfect vision: an apparatus for refraction, formed by the transparent ocular media; a muscular diaphragm, formed by the iris, for the regulation of the amount of light passing to the retinal surface; an apparatus for accommodation (the ciliary muscle and crystalline lens) which adapts the eye to varying distances; muscles which turn the eye in the varying directions of external objects; and, lastly, the protective apparatus furnished by the *tutamina oculi* above described.

Light.—Light is the normal physiological stimulant of the retina, but any stimulant (mechanical, physical, or chemical) that acts on the retina and optic nerve, causes, even in perfect darkness, a luminous sensation.

Light is due to the vibrations of æther, and the direction of these vibrations correspond to the direction of the *luminous rays*. The vibrations are transverse, that is to say, they are perpendicular to the direction of the rays of light. The transmission of light in the air takes place at a velocity of 300,000 kilometres per second, and from each luminous point as centre, an infinite number of rays pass in all the directions of space. The duration of the vibrations influences the sensation produced by them, and color is for luminous sensation, what height is for sound. The inferior limit of visible vibrations is caused by the color *red*, which gives 435 billions of vibrations per second; the superior limit is that of violet, which corresponds to 764 billions. Beneath 435 billions the retina is not impressed, although the vibrations are able to produce heat (*calorific rays*); above 764 billions the retina is insensible, although these (*chemical rays*) can affect certain substances (nitrate of silver). The ultra-violet rays can sometimes impress the retina, so as to become visible, if they are observed under certain conditions, so as to increase their intensity.

The laws of *reflection* and *refraction* need not be tabulated, as they belong rather to a treatise on optics.

In its passage to the retinal surface, the light has to traverse the following structures: cornea, aqueous humor, anterior part of capsule of crystalline lens, lens itself, posterior layer of lens-capsule, and vitreous humor.

Formation of the retinal image.—The images of external objects are formed on the retina. This can be demonstrated by removal of the posterior part of the sclerotic from the fresh eyeball of an animal, and placing the eye in the opening of a darkened chamber. Also, if an individual be taken into a darkened chamber and a candle be held close to the eye, in front and to the outer side, while the eye is rotated outwards, the image formed on the inner side of the retina will be seen *through* the sclerotic. The retinal image can also be observed directly by means of the ophthalmoscope.

The point of the retina impressed by the image of any point on a body at a distance, is the one that corresponds to the line drawn from the latter to the retina, and passing through the nodal point of the eye.

When the luminous point approaches the eye (within a distance of twenty metres or so) the rays of light, if the optical

conditions remain the same, will fall at some distance behind the retina, and vision is no longer distinct.

If the luminous point be not situated in the optic axis, but in one of the secondary axes of the eye, the focus is still on the retina, and as the line passing from the luminous point has to pass through the nodal point of the eye, the position of the image is always on the opposite side of the retina. To this physical fact is due the *inversion of the retinal image*.

The angle included between the extreme rays of a luminous object is the angle under which an object is seen (*visual angle*). The magnitude of the angle depends on two conditions: the size of the object, and its distance from the eye. At equal distances the size increases with the size of the object; the objects being of equal bulk, it diminishes, as the distance increases.

The minimum visual angle is sixty seconds; below this limit the extreme points of an object are no longer separate, and but one point is perceived. This minimum visual angle corresponds to a retinal image of about .004 mm., which is nearly the diameter of one of the retinal cones.

The *acuteness* of vision is in inverse ratio to the visual angle; it diminishes as the latter increases. The size of the smallest retinal images varies with different individuals; the retinal images of extremely small size, such as those of the fixed stars, are still perceptible, although they impress but an infinitesimal point of the retinal surface. In favorable conditions, bodies having a diameter of $\frac{1}{40}$ th to $\frac{1}{100}$ th of an inch, are perceived by the naked eye. Round bodies can be seen under an angle of 20—30 seconds; threads, at 3 seconds; and for bright threads the angle falls to $\frac{1}{2}$ sec. or even less.

We have now established the following characters of the retinal image:—

- (1) It is inverted;
- (2) It is distinct when the different points of the object form their focus exactly on the retina;
- (3) The size depends on the visual angle.

Circles of diffusion.—When the rays of light proceeding from a luminous object do not come to a focus directly on the retina, the image is no longer distinct, and *circles of diffusion* appear around it. In the normal condition the luminous rays passing to a point of the retina through the pupil form a cone,

the base of which is at the pupil, and the apex at the retinal focus. But if the focus be placed in front of or behind the retina, the latter intersects the bundle of rays, so that instead of a point on the retina corresponding to one on the luminous object, we have a circle formed. Also, the different points of the retina will be intersected by rays coming from various parts of the object, and the image in this way becomes blurred, and loses its distinctness.

The existence of these circles of diffusion explains why it is that we cannot, at the same time see clearly, objects which are placed at different distances from the eye. Their size varies with the distance of the focus from the retina, being larger as the distance is greater, and also with the size of the pupil, contraction of which narrows the cone of luminous rays, and, consequently, the circles of diffusion.

Scheiner's experiment.—If two holes are pierced in a card nearer than the breadth of the diameter of the pupil, a pin vertically placed and viewed through these holes appears single at a certain (short) distance, but forms a double image if nearer or farther than this point.

Emmetropia.—In the normal, or emmetropic, eye the principal focus is found at the retina, and the rays which come from all distances converge to the surface of that membrane. When the rays are not focussed on the retina; the eye is said to be *ametropic*. Two varieties of *ametropia* are known: (1) *myopia*, where the antero-posterior diameter of the eye-ball is increased, and the rays are brought to a focus in front of the retina; (2) *hypermetropia*, where the antero-posterior diameter is diminished, and the focus is placed behind the retina.

In the emmetropic eye, the furthest point of distinct vision (*punctum remotum*), is at an infinite distance. Within this range, and down to a distance of about sixty-five metres, the rays of light coming from an object may be regarded as parallel, and converge to a retinal focus. But at shorter distances than this the focus falls behind the retina, and the intervention of accommodation is necessary for distinct vision.

For a myopic eye, the *punctum remotum* is situated at a distance, which varies according to the degree of myopia. At this distance, vision is perfect without accommodation. Between this range and infinite distance, the use of a biconcave lens is necessary for the formation of a distinct retinal image.

In hypermetropia the punctum remotum does not exist ; the rays from the greatest distances are focussed behind the retina, and accommodation is essential in every case for the formation of a distinct image. This can only be done by the aid of a biconvex lens. In water the eye becomes enormously hypermetropic, and, in case of fishes, accommodation is maintained by the great convexity of the lens.

The degree of ametropia is easily measured by finding the refracting power of the lens which renders the eye emmetropic.

The distance of the punctum remotum is measured by the focal length of the lens which renders the vision of an object distinct (when placed at a distance proportioned to the size).

Spherical aberration.—We have supposed, up to the present, that the parallel rays coming from infinite distances come to a focus at a single point on the retinal surface. This is not, however, absolutely correct, as the rays which pass through the crystalline lens, near its margin, undergo a greater degree of refraction than those which pass through the centre. This physical law prevents the uniform arrangement of the foci on the retina, and so produces spherical aberration, of which two varieties exist : *transverse* and *longitudinal*.

In *transverse spherical aberration* we have a series of foci formed by the rays entering the points of the various circumferences on the anterior surface of the crystalline lens, of which the common centre is in the primary visual axis. From the regularly increasing refraction of the more external rays the foci will be arranged in a linear series on the visual axis, of which the most anterior will be that formed by the rays from the most external circumference.

Longitudinal spherical aberration is due to the rays coming from the same *meridian* not coming to a single focus. This form of aberration may exist for the different points of the same meridian, or for the different meridians with regard to one another. This latter condition is the one described by Young, under the name of *regular astigmatism*. The other variety of longitudinal spherical aberration is the *irregular astigmatism* of oculists.

Another condition which may complicate still more that of spherical aberration, is the non-parallelism of the curves on the front of the cornea and of the crystalline lens.

The transverse aberration of sphericity, and the irregular astigmatism are corrected, by the following dispositions of the dioptric media.

(1) The iris intercepts the external rays of light which would be too powerfully refracted.

(2) The curve of the cornea is not spherical, but approaches that of an ellipsoid, so that the external rays of light undergo less deviation.

(3) The lens presents successive layers, of which the refracting power diminishes towards the circumference; this also ensures less deviation from the original direction.

Regular astigmatism may exist for the cornea or lens, or both, and in the latter case they may either be compensatory, or (as oftener happens), they may be so disposed as to cause an increase of the aberration.

As a rule, the vertical meridian of the cornea has the smallest radius and the greatest refracting power. The condition may be demonstrated by drawing a vertical and a horizontal line on a piece of paper meeting at a right angle. If astigmatism exist, they cannot both be distinctly seen at the same time. A number of radiating lines may be drawn from the same centre for the purpose of testing the different meridians.

Chromatic aberration.—We have hitherto supposed that the eye was absolutely achromatic, but this is not at all the case, even in the normal (emmetropic) organ. A ray of white light in passing through a biconvex lens is decomposed into the seven colors of the spectrum. This decomposition by the lens of the human eye is compensated for by the other dioptric media, so that, in ordinary conditions, the achromatism of the eye appears to be complete for the distance of clear vision. It is not so, however, at a distance greater or less than that of distinct vision.

The tendency to chromatism explains the fatigue experienced, when we look attentively at the same time on objects of different color. If we look closely at red letters on a blue ground, the letters or the ground appear to be agitated.

Entoptic phenomena.—As the dioptric media (including the anterior layers of the retina itself), are not entirely transparent, some rays of light are often intercepted so as to cause the appearance of small opaque objects floating into the field of vision (*muscae volitantes*).

Absorption and reflection of light in the eye.—When the rays of light have passed through the dioptric media to the retina, and made the necessary impression on the bacillary layer, the physiological function of vision is fulfilled. But it is still interesting to inquire what becomes of these afterwards. The great part is absorbed by the choroid coat and transformed into heat (?); but a considerable proportion is reflected and leaves the eye again. This reflection appears at first incompatible with the dark color of the pupil, but the latter appearance is explained by remembering that in looking at the eye of another the retina of the observer does not furnish any light to the other, so that the latter has no rays to send in that direction, as reflected rays always return to the point from which they came.

The red color of the pupil of an albino is due to the absence of pigment from the sclerotic and choroid, which allows those coats to be traversed by the rays of light, and those rays, being reflected through the pupil, arrive at the eye of the observer. If a card pierced with a hole of the size of the pupil be placed before the eye of an albino, the pupil seen through this aperture appears dark like that of other eyes, because the lateral rays of light are shut off from the eye.

The ocular light becomes visible to the eye of an observer when the eye is myopic, or not accommodated for the source of light. In this case, the image of the luminous body, and of the pupil of the observer, are not perfectly defined on the retina; images of diffusion result, and, if these partly coincide, the pupil of the observer's eye receives some of the rays reflected from the other.

On the fact of the ocular reflection is based the use of the ophthalmoscope (Helmholtz, 1851).

Accommodation.—When a luminous body approaches the eye too nearly, the rays which pass from it tend to come to a focus behind the retina. On this account circles of diffusion would form, preventing the appearance of a distinct image, if a special apparatus did not exist for the purpose of modifying the degree of refraction. This modification is what is understood by the term accommodation.

That such a mechanism is necessary for viewing objects at different distances is easily shown. If two needles be placed upright in a piece of card, and the eye be placed in the same

right line, we find that both cannot be distinctly seen at the same time ; when one is distinct the other is not so, because one always forms an image of diffusion on the retina.

The emmetropic eye at rest is disposed to see objects at an infinite distance, and we are conscious of no effort till an object is brought within a moderate distance of the retina (65 metres, Lesting). Within this range we are conscious of a sense of effort, which becomes greater as the object approaches the eye. The *punctum proximum* (nearest point of distinct vision) is about twelve centimetres from the cornea.

The *punctum remotum*, accordingly, corresponds to repose of accommodation, and the minimum refracting power of the eye ; the *punctum proximum* to the maximum of accommodation, and the maximum of refracting power. The distance between these points is the *latitude of accommodation*.

About the age of forty the power of accommodation diminishes ; the *punctum proximum* recedes from the eye, and the latitude of accommodation decreases. When the distance of the *punctum proximum* is more than twenty-two centimetres, *presbyopia* is said to exist. At seventy years the power of accommodation has fallen to zero.

Mechanism of accommodation.—There is no doubt that the lens takes the leading part in the mechanism of accommodation, and this power is completely lost after its removal (*aphakia*). In adaptation of vision to near distances the lens becomes more convex, and its refractory power becomes greater. The active agent is the ciliary muscle, and the following explanation of its action is due to Helmholtz : “in the normal state the anterior surface of the lens is flattened by the pressure of the zonula of Zinn (if this membrane be incised the convexity immediately increases). The radiating fibres of the ciliary muscle (*tensor choroideæ*), by drawing forward the anterior part of the choroid, relax the tension of the zonula, and the pressure is taken off the anterior surface of the lens, which immediately becomes more convex ; at the same time, the insertion of the iris is drawn a little backwards.

The following phenomena accompany accommodation :—

(1) The curve of the anterior surface of the cornea increases ; for the maximum accommodation, the radius diminishes from 10 to 6 mm. The curve of the posterior surface also increases, but only to a slight extent (the radius falling from 6 to 5.5 mm.

(2) The pupil contracts ; the pupillary margin of the iris is pressed forwards, while the attached margin is retracted. The narrowing of the pupil takes place after the change of form of the lens (Donders).

(3) The intra-ocular pressure increases in the posterior part of the eye. According to H. Müller, the circular fibres of the ciliary muscle (*compressor lentis*) increase the convexity of the lens, by direct pressure on its circumference. The movements of accommodation are governed by the third nerve. Hensen and Voelckers have obtained movements of accommodation by direct stimulation of the ciliary nerves.

Movements of the iris.—The iris represents a true diaphragm, which regulates the amount of light passing into the retina. The pupil is placed a little to the inside of the centre ; the visual axis forms an angle of 5° with the optic axis. The nervous supply of its muscular fibres has been already mentioned.

The usual stimulant which determines contraction of the pupils is the access of light to the retina. If light be applied to one eye only, both pupils contract, but that of the stimulated side to a somewhat greater degree.

Internal rotation of the eyeball is accompanied by contraction of the pupillary aperture ; the two conditions co-exist during sleep. It is also contracted in accommodation for near objects.

Retinal Stimuli.—Light is the normal specific stimulant of the retina, and the only one called into play in the fulfilment of its physiological functions. It is, however, susceptible to the action of other stimuli (mechanical, chemical, electrical, &c.), all of which are found to elicit luminous sensations only.

Pressure on the globe of the eye causes luminous appearances (*phosphenes*) which were carefully studied by Morgagni. When the closed eye is pressed by the point of the finger, near the orbital margin, a luminous appearance is observed on the opposite side of the eye. A moderate, uniform pressure causes the appearance, in the field of vision, of brilliant luminous images of indefinite and rapidly-varying shape (*Purkinje's figures*). A rapid change of the position of the eyes sometimes causes an appearance of fiery rings or crosses in the region of the optic papilla. If in the dark, the eye is first accommodated for near vision, and then suddenly changed as

if for distant vision, there appears, in the visual field, a circle of fire which disappears as a star (Czermak's *phosphene of accommodation*):

Stimulation of the optic nerve causes the same phenomenon; when the optic nerve is divided, large masses of light are seen at the moment of section.

Punctum cæcum.—The existence of a blind spot on the retinal surface was first shown by Mariotte (1669). If the thumbs be held together opposite the eyes, and the left eye kept closed, while the right eye is fixed on the left thumb, the right thumb, on being moved slowly from the other, is lost to sight at one point, but is again visible when moved a little further off. If the image of a flame be reflected by the ophthalmoscope directly on the optic disc, no luminous sensation is observed by the individual examined.

How the blind spot is filled (in vision with one eye) is not very clearly understood, but there can be no doubt that it is done by an unconscious intellectual operation, for, as Volkman has pointed out, in modifying Mariotte's experiment by examining a printed page, the blank, corresponding to the blind spot, is covered with letters which we do not see.

Yellow spot.—This is the centre of direct vision, and is distinguished from other parts of the retina (especially at the fovea centralis) for the distinctness of the images formed there. Beyond the yellow spot, the clearness of vision over the lateral parts of the retina diminishes as the ora serrata is approached, but this diminution is not uniform; it is slowest for the external region, and presents variations in different individuals. At the angle of 60° from the axis of vision, an object, to form a visible image on the retina, must have a diameter 150 times that required when the yellow spot is engaged.

Membrana Jacobi.—It is known that the rods and cones of the bacillary layer are the only retinal structures which receive luminous impressions, although the exact way in which these elements are affected by light cannot be clearly made out.

Retinal purple: retinal rouge (Kühne).—The outer ends of the rods of the membrana Jacobi contain during life a red coloring matter (Boll), to which the above names have been applied. It may be extracted by a solution of the biliary acids; is decolorised during light, and regenerated in darkness at the expense of the subjacent epithelium (Kühne). As it is very

rapidly destroyed by exposure to light, especially in mammals. it is necessary in preparing it to use sodium light. If a separated eye be placed with necessary precautions before a clear window, photographic impressions of external objects (Kühne's *optogrammes*) are obtained, the luminous parts being reproduced in white, and the dark portions in red on the retina. These images may be fixed by a solution of alum. This *visual purple* is present in all vertebræ, except the pigeon, the common fowl, and in serpents which have but cones. It is *never found in the cones*, and is accordingly absent from the yellow spot, which destroys the idea advanced, at the time of its first discovery, that it was of great importance in the stimulation of the retina by light.

Conditions of retinal stimulation. (a) *Duration.*—In order to produce an impression, the stimulus must act on the retina for a certain length of time; if the time is too short, no luminous sensation results. This may be shewn by experimenting with rotatory discs having alternate sectors of different colors.

(b) *Intensity.*—If the retinal stimulus is not sufficiently strong, there is no luminous sensation produced; and, on the other hand, when the intensity is very great, we are dazzled, and the luminous sensation is replaced by a vivid sensation of pain. The *minimum* sensation necessary for distinct vision varies in different individuals, and the standard is lowered by rest. It has been shewn by experiment that light, one-millionth of the strength of ordinary day-light, is sufficient to impress the retina (Aubert).

Persistence of retinal impressions.—The impression follows instantaneously the exposure to light, and if a latent period exist, it is so short that it has been found impossible to demonstrate. When established it persists for a short period ($\frac{1}{30}$ — $\frac{1}{10}$ sec.) after the removal of the stimulus. If in looking at a bright light we rapidly shut and re-open the eyes, we are not conscious of light. If a lamp is suddenly extinguished in the dark, we continue to see a luminous image of the flame for a short time (this is called the *consecutive image*, or *positive accident image*). If a lucifer match, with one end lighted, be rapidly whirled round, it forms a continuous circle of fire, and if a white spot be marked on a black disc, and the latter rapidly rotated, we see a grey ring which appears to be immobile.

Numerous toys have been constructed on this principle: the

thaumatrope of Paris, *stroboscopic discs* of Stampfer, *phenakistiscope* of Plateau, &c., &c.

Irradiation.—It is well-known that very brilliant surfaces appear more extensive than they really are, and on this account that a luminous sensation is not proportional to the intensity of the light which produces it. A fixed star appears as a small bright surface; a white square on a dark ground appears larger than a black square on a white ground. "All these phenomena," says Helmholtz, "are referable to the fact, that the margins of the bright surfaces appear to advance upon the visual field, and to encroach upon the dark surfaces which surround them." The phenomena of irradiation are more pronounced when the accommodation is incomplete.

Fatigue of the retina.—As in the case of motor and sensory nerves, a diminution of the excitability is observed after prolonged stimulation; and, on this account, intermittent stimulation of the retina is more effective than continuous. This fatigue of the retina explains the greater sensibility of the membrane after spending some time in darkness.

Consecutive images.—We have already alluded to the formation of these images, which are due to persistence of the retinal impressions. They are of two kinds, *positive* and *negative*. In the former, the light and dark parts of the object are represented as such in the image; in the latter, the clear parts are dark, and *vice versa*, as in the negative of a photograph.

If while the positive image is still visible, we look towards a very clear surface, the negative image appears. The more powerful the stimulus, the better marked is the positive image; but for the maximum effect, the duration of the stimulus should not be beyond a third of a second. With the negative image, on the other hand, the duration is greater in direct proportion to that of the luminous action.

The positive images are explained by persistence of the retinal stimulation after the removal of the stimulus; the negative images are, on the other hand, due to fatigue, and diminution of excitability of the retinal surface.

Colors.—The word color is used in three different senses: (a) in one case it denotes a special sensation produced by a peculiar stimulation of the retina (the color red, the color blue, &c.); (b) it is applied to the æthereal vibrations which produce it (red rays, violet rays, &c.); (c) the term is applied to the mode

in which the surface of an object behaves under the influence of light—it is in this sense that we speak of the color of an object.

The solar spectrum presents seven primary colors : violet, indigo, blue, green, yellow, orange, and red. Between these are an infinity of shades, but the colors are all referable to four principal ones, which occupy definite regions of the spectrum : red, yellow, green, and blue.

Besides these simple colors, there are *compound* ones formed by a mingling of the shades of two or more of the others. These colors are called *complementary*, which, when mingled, two by two, produce a white. The following table gives the complementary colors of the spectrum :—

Red.	Greenish blue.
Orange.	Prussian blue.
Yellow.	Indigo blue.
Greenish yellow.	Violet.
Green.	Purple.

Green alone has no complementary color in the spectrum ; it gives white with the compound color, purple. A mixture of more than two simple colors does not give a new tint ; the possible colors are exhausted by mixture of the simple colors, two by two.

White light was first decomposed by Newton, with the aid of the prism, into its spectral constituents. He also demonstrates the synthesis of white from the hues of the spectrum, by the well-known experiment of painting on a disc, divided into proportional sectors, the primitive colors in their order. When this disc is rapidly rotated, the resulting sensation is that of a uniform white. Several other devices have been employed for the purpose of mingling the different colors.

Sensations of color.—In the sensations of color there are three chief characters : *tone*, *saturation*, and *intensity*.

(a) The *tone* of a color depends on the number of vibrations of the æther (or length of the wave of undulation). It corresponds to the height of an auditory sensation.

(b) A color is said to be *saturated* when it does not contain white light, as in case of the simple colors of the spectrum, and purple. We can accordingly diminish the saturation of a color by gradual addition of white.

(c) The *intensity* of a color depends on the amplitude of the

vibrations. It diminishes from the pure spectral colors to black by a graduated scale. When it passes a certain intensity, the tone of the color disappears, and a sensation of white alone remains.

In a strong solar light, the impression of yellow predominates ; in a faint solar light it is blue, the complementary of yellow ; in ordinary artificial light, the tint is yellow, so that blue objects are more deeply colored, while yellow objects appear paler.

Fundamental colors.—Brewster believed that all colors were derived primarily from three : *red, yellow, and blue*. This, however, is incorrect, for there are not three colors from the mingling of which the other spectral hues can be derived. Young put the subject in a more plausible form, by suggesting for the explanation of the phenomena of colors, that they are all referable to three *fundamental sensations* : those of *red, of green, and of violet*. Corresponding to these sensations, three kinds of retinal nerve-fibres are supposed to exist, of which the stimulation gives rise to sensations of red, green, and violet respectively. Also, it is supposed that white light stimulates these fibres with different degrees of activity, according to the length of the wave. The longest wave acts most on the fibres which correspond to the red color ; the medium wave on the fibres of green ; and the shortest on the fibres of violet.

This theory of Young has been adopted by Helmholtz. It is also supported by the facts of *dyschromatopsy*, in which there is an inability to distinguish one or more of the fundamental colors. The commonest form of this defect is that in which red is the invisible color (Daltonism), and in the compound colors into which red enters, the complementary color is alone visible (white appearing a bluish-green, &c.)

Arguing from the structure of the yellow spot, and from the absence of the cones in nocturnal animals, Schultze has been led to believe that the cones are the structures affected by color, while the rods only serve to distinguish the different degrees of clearness and obscurity. According to Charpentier, the structures affected by color do not lie in the posterior part of the retina at all.

Movements of the eye-ball.—The globe of the eye, with regard to its movements, represents a true enarthrodial joint, and its displacements follow similar laws.

The *centre of rotation* of the eye-ball is found a little behind

the optic axis (about 1.75 mm.) The *point of regard* (point of fixation) is that towards which the eyes are directed in normal vision. The *line of regard* is a line drawn from the point of regard through the centre of the eye-ball. The *plane of regard* is that which passes through the two lines of regard.

The movements of the eye-ball are chiefly around three principal axes of rotation : *antero-posterior, vertical, and transverse.*

The following table gives the movements produced by the ocular muscles :—

<i>Inwards</i>	.	.	.	.	Rectus internus.
<i>Outwards</i>	.	.	.	.	Rectus externus.
<i>Upwards</i>	.	.	.	.	{ Rectus superior. Obliquus inferior.
<i>Downwards</i>	.	.	.	.	{ Rectus inferior. Obliquus superior.
<i>Inwards & upwards</i>	.	.	.	.	{ Rectus internus. Rectus superior. Obliquus inferior.
<i>Inwards & downwards</i>	.	.	.	.	{ Rectus internus. Rectus inferior. Obliquus superior.
<i>Outwards & upwards</i>	.	.	.	.	{ Rectus externus. Rectus superior. Obliquus inferior.
<i>Outwards & downwards</i>	.	.	.	.	{ Rectus externus. Rectus inferior. Obliquus superior.

Binocular vision.—The fact that the impression of a single object only is conveyed to the mind, although images are formed on both retinae, is usually explained by supposing the existence of *corresponding points* of the two retinae, simultaneous stimulation of which is conveyed to the same part of the sensorium. It has also been suggested that we use but one eye at a time for ordinary vision.

Another explanation is by the *theory of projection*, which supposes that the retinal image is projected into space in the direction of the visual line, and that the position of the resulting image is determined by the intersection of the visual lines of the two eyes. This theory also explains why we do not see inverted images.

Distance.—Distance can be estimated even by monocular vision. The apparent size of the object is one of the great guides in this case (due to the visual angle). The clearness of the image conveyed to the eye, and other minor details, also

assist in forming our judgment. In binocular vision, the degree of convergence of the eyes (estimated by the *muscular sense*) is also a guide.

Direction.—As the retina is distinctly spherical, right lines when of a certain length, always present a curvature. The upper surface of a straight line held opposite the eye presents a concavity. The judgment of direction of lines is not made in the same way for the two eyes. If a vertical and horizontal line intersect at a right angle, on examining with the right eye, the superior right and inferior left angles appear (to most individuals) to be obtuse, and the others acute; while the opposite occurs with the left eye.

Solidity.—The estimation of solidity is essentially the same as the perception of depth. E. Brücke supposes that it is due to the necessity for passing the eyes over the different parts of the surface of a body, so as to receive successively, on the identical points of the yellow spot, the images of all the points on its outlines. Dove has, however, shown that double and stereoscopic images are fused in the instantaneous illumination of the electric spark. Hering has supposed that the estimation of solidity is altogether due to a peculiar form of retinal sensation, and not to any mental act, but his theory has not been substantiated.

CHAPTER XIX.

REPRODUCTION.

ALL living organisms possess the power of reproducing their kind. The process of reproduction or generation may be either *sexual* or *asexual*. It is unnecessary for us to discuss the vexed question of *spontaneous generation* in the present work.

Asexual generation (*monogony* of Hæckel) is merely a mode of growth, and might be referred to the phenomena of the general nutrition of organisms. The simplest form is by *budding*, in which on one point of the surface of the generating organism an organised swelling forms, which gradually develops to form a new organism similar to the first. Once formed, it may either remain attached to the parent (as in case of the coral) or drop off and lead an independent existence, as in case of the hydra.

Another variety occurs in *fission*, by which the generating organism divides into two halves, each of which forms an individual exactly like the original. It occurs in some of the infusoria, &c.

The third form of asexual generation is that by *germs* or *spores* (Hæckel's *sporogony*), which is truly an internal budding (*endogenous formation*). A germinating cell forms in the interior, which is afterwards set at liberty, and gradually develops to a perfect organism.

Sexual generation.—In the higher animals, the union of two elements furnished by distinct individuals, is essential for the development of a new organism. Of these two elements, one is furnished by the male (*spermatozoon*), and the other by the female (*ovum*). The union of the two elements constitutes *fecundation*. After fecundation the ovum develops and forms the embryo. In some forms of animal life both elements are formed by the same individual (*hermaphroditism*).

Ovum.—The ovum is developed in a special organ called the ovary. That of the human female is a cell of about $\frac{1}{160}$ th of an inch in diameter, with a distinct investing membrane (*zona pellucida*, *vitelline membrane*). The contents form the

vitellus (yolk). Within is a large eccentric nucleus (*vesicula germinativa* of Purkinje), which, in turn, encloses the nucleolus (*macula germinativa* of Wagner). In some of the inferior animals, there is found within the latter a granule (*nucleolus* of Schrön, *punctum germinativum* of Hæckel), but it does not appear to exist in mammals. The præmordial ovum (*protoovum*) is formed by a small mass of protoplasm surrounding the nucleus. This mass is the *germ-yolk*, and the elements just mentioned are the only ones present in many of the inferior animals. The addition part of the vitellus (*food-yolk, deutoplasma* of v. Beneden) is a later formation. Where the food-yolk and germ-yolk are not distinctly separated, the ovum is said to be *holoblastic*; in other cases it is *meroblastic*.

An *embryogenic vesicle* (*nucleus vitellinus* of Carus) develops close to the ovum (from one of the epithelial cells which surround the latter in the Graafian vesicle). According to Balbiani, it is analogous to a male element, and, when developed, penetrates into the ovum, where its entrance gives rise, by an unknown change, to a power of evolution not previously possessed (*præfecundation*). This *præfecundation* may go on to the first phases of development, and in some cases it may proceed to the formation of organisms capable of reproduction without the intervention of a male element (*parthenogenesis, Lucina sine coitu*). This is illustrated in the generation of *aphides*, &c.

Spermatozoon.—This, the male element, is developed in the testicle. It is of well-known tadpole shape, and presents a *head*, an *intermediary segment*, and a *tail*. It presents during life very active movements. According to the researches of Balbiani, the functional activity of the spermatozoon is preceded by the entrance of a cellular structure analogous to the female ovum, so that in both sexes, according to this observer, a true *histological hermaphroditism* exists. The cells of the tubuli seminiferi, from which the spermatozoa are developed, are called *spermatoblasts*.

Fecundation.—This process consists in the passage of the male element (*spermatozoon*) into the female element (*ovum*). The ova of the human female are found at birth in large numbers near the surface of the ovary, and undergo no special change till puberty arrives. Some are then seen to pass into a state of maturity, and are ready to be discharged into the Fal-

lopian tube. The ripening ovum first sinks deeper into the ovary, then once more approaches the surface, where it is received, on bursting of the Graafian vesicle, into the fimbriated extremity of the Fallopian tube. Three well-marked phenomena accompany the maturation of the ovum: disappearance of the germinal vesicle, formation of the *polar-globules*, and formation of the *ovular nucleus*.

According to the latest researches (Butschli, Hertwig, Fol, &c.) the germinal vesicle is changed into a fusiform body (*amphiaster* of Fol), which presents a system of rays (*aster*) at each end. This body moves towards the periphery, when the star next the surface projects, and forms the *polar globule*. The remaining part forms a complete amphiaster, which in its turn forms a second polar globule.

The polar globules are, according to some, merely excrementitious bodies. Others think that they exercise a special influence on the direction of the subsequent segmentation.

The formation of the ovular nucleus (*female pronucleus* of Van Beneden) is from that part of the fusiform body which has not contributed to the polar bodies.

The ovum, so prepared, is penetrated by the spermatozoon, which passes in through the zona pellucida. In some animals, especially fishes, a *micropyle* exists for its transmission (Martin Barry, Keber). The first change following the fecundation is the formation of the *spermatic nucleus* of Hertwig (*male pronucleus* of Van Beneden). It is probably formed by fusion of the head of the spermatozoon with a part of the protoplasm of the ovum. This body soon becomes surrounded by radiating filaments (*male aster* of Fol). The male and female pronucleus then unite to form the *nucleus of segmentation*.

Evolution of the ovum subsequent to fecundation.—After the changes above described, the ovum consists of *vitelline membrane*, *vitellus*, and *nucleus of segmentation*. The vitellus then proceeds to divide; first into two parts, then into four, eight, &c. The agglomeration of vitelline globules resulting from this division forms the so-called *mulberry mass* or *morula*. By degrees fluid is found to collect in the centre, and the globules are pushed towards the circumference, where they form an investing layer (*blastoderm* of Pander, *blastodermis vesicle*, *blastula*). The next change is the separation of the blastula into two layers, *ectoderm* and *entoderm*. From the former is

developed the epidermis, cerebro-spinal axis, and organs of special sense ; from the latter come the tissues of the alimentary canal, and the annexed structures.

Between these two layers soon appears a third, the *mesoderm* (*mesoblast*) of which the mode of formation is not yet fully determined. This in turn divides into two layers, of which the outer joins the epiderm to form the *somato-ploure*, while the inner joins the entoderm to form the *splanchno-ploure*.

In vertebrates, all four layers are united at an early period over the *area germinativa*, which corresponds to the place of the future body. It is at first of circular form, but afterwards becomes elongated, with lateral constrictions. Its central portion becomes transparent (*area pellucida*), while the surrounding remains opaque (*area opaca*).

The first trace of the embryo appears at the posterior part of the *area pellucida*, as a shallow longitudinal groove (*primitive trace*).

We do not purpose entering into a history of the development of the embryo, which the researches of later years have raised to the rank of a new and extensive science. The connection of the various parts of the organism with the blastoderm is as follows :—

(a) From the *epiblast* are developed the epidermis and its appendages, the cerebro-spinal axis, the chief parts of the eye, ear, and nose.

(b) From the *hypoblast* is formed the epithelium of the alimentary canal (excepting the mouth) ; also of the lungs and gland ducts.

(c) From the *mesoblast* are derived the skeleton, muscles, fasciæ, tendons, nerves, true skin, connective tissues, the vascular system, the blood, the muscular and fibrous coats of the alimentary canal, and visceral passages, serous membranes, parenchyma of glands, and genito-urinary organs (Allen Thomson).

Semen.—The semen is secreted by the testicle, but is not ejaculated in the pure form, being mingled with the secretions of the prostate, of Cowper's glands, and of the vesiculæ seminales.

Pure semen is a thick, ropy fluid, of a whitish or amber color, without any odor, and having a neutral or slightly alkaline reaction. The microscope shows the presence of spermatozoa.

Ejaculated semen is a clear, ropy fluid, with whitish opaque flakes. It has a characteristic odor, saline taste, and feebly alkaline reaction. Its specific gravity is higher than that of water. After ejaculation it coagulates spontaneously, but soon liquefies.

The semen contains albuminoids (albumin, albuminate of potash, spermatin, and mucin), cholesterin, nuclein, cerebrin, protagon, and cholesterin (probably from the spermatozoa), fats and mineral salts, especially chloride of sodium and phosphates. On addition of water it gives a mucous sediment; boiling causes no turbidity; alcohol coagulates it completely. On slow evaporation, it leaves prismatic crystals (Robin).

The following analysis of the semen of man is by Vauquelin; the others are by Kolliker :—

In 1,000 parts.				Man.	Bull.	Horse.
Water	..	..	..	900	822.13	819.40
Solids	..	..	..	100	177.87	190.60
Spermatin and extractives	..	..	..	60	150.89	164.49
Fat	..	..	..	—	21.60	—
Salts	..	..	..	40	25.96	16.11

Spermatin is closely connected with albuminate of potash and mucin. Its solution is not coagulated by heat, but is made turbid by acetic acid; this turbidity disappears on adding an excess. It gives a precipitate with ferrocyanide of potassium.

The spermatin secretion commences about the age of 12—15 years, but spermatozoa do not usually appear till 16 or 17. It then continues to a very old age, while it still contains spermatozoa, although in diminished number. The color is darker in old age from the presence of greyish patches (*sympexions*), which come from the vesiculæ seminales.

The *prostatic fluid* is white, milky, alkaline in reaction, and contains 2 per cent. of solids; chiefly albuminoids, and chloride of sodium.

The secretion of Cowper's glands is a ropy, viscid fluid, of alkaline reaction.

According to Robin, the spermatin odor does not exist in

any of these fluids, and is developed only at the moment of ejaculation.

The movements of spermatozoa, after emission, are very active, and, according to Marion Sims, they are able to ascend, in three hours, from the hymen to the os uteri. They are vigorous enough to displace calcareous particles ten times their size. These movements persist for seven or eight days in the genital organs of the female, and they have been found to exist in the body twenty-four hours after death. These movements are favored by the normal secretions of the sexual organs, and by weak alkaline solutions; they are stopped by alcohol, æther, chloroform, creasote, acids, metallic salts, concentrated saccharine solutions, electricity, extremes of temperature, also by great acidity or alkalinity of the utero-vaginal secretions. Among indifferent substances are: chloride of sodium, sugar, urea, albumin, glycerine, narcotics, &c., except their solutions are too dilute or too concentrated.

Ovulation.—The female ovary continues to discharge ova at intervals between the ages 15 and 45 years. Every twenty-eight days, on an average, an ovum escapes into the Fallopian tube, by which it is carried into the uterus. The discharge of the ovum is accompanied by certain genital phenomena, of which the most obvious is that of menstruation.

A Graafian vesicle approaches the surface of the ovary, on which it projects; the prominent part then becomes thinner till rupture at last takes place. The ovary is much congested at this period, and at the time of the escape of the ovum some blood escapes into the follicle.

Menstruation.—This phenomenon is usually associated with the discharge of an ovum, but not always. The mucous membrane of the uterus becomes congested and hypertrophied; the epithelium is then detached, and sometimes portions of the membrane as well; the capillaries are exposed, and an oozing of blood takes place, which constitutes the menstrual flow. It lasts about 3—5 days; the quantity of blood is about 100—200 grammes. The discharge is at first serous; towards the end it assumes the characters of mucus. Menstrual blood is seldom coagulable except when the quantity is copious.

Puberty.—The commencement of the period of fecundity in the female, which occurs about the age of fifteen, modifies not only the genital organs, but acts on all parts of the system. It

is accompanied by development of the mammary glands, of the larynx, growth of pubic hairs, and the deposit of a layer of subcutaneous fat over the whole surface.

Menopause.—The cessation of ovarian activity in the female takes place between the ages of forty-two and fifty. Its occurrence is generally gradual; the menses cease for a little, and then reappear, and this transition period lasts from six to eleven months. The change of life acts upon the uterus, and the ovaries become atrophied; the external genital organs lose their excitability; the breasts shrivel, the timbre of the voice becomes more accentuated, &c.; and, in general terms, the sexual characteristics diminish, and tend to disappear.

Discharge of the Ovum.—It is difficult to understand how it is that the mouth of the Fallopian tube comes to grasp the portion of the ovary where the ovum is about to escape, and some have suggested that the friction of the *morsus diaboli* is the determining cause of the rupture of the Graafian vesicle. After the extirpation of one ovary, and the Fallopian tube of the opposite side, the ovum was found to descend along the other Fallopian tube (Leopold).

The time spent in the tube is nearly impossible to determine, but from collected observations it would seem to vary from two to ten days (Marion Sims).

Coition.—In order that fertilization of an ovum should take place, the introduction of spermatozoa into the uterine cavity is necessary; this takes place during the act of coition. Before coition can be effected the penis must have assumed a certain state of rigidity (*erection*). In this state the organ reaches a size four or five times that of the quiescent state; it becomes firm and rigid, and presents a curve which corresponds to that of the vagina. The temperature is elevated, and the sensibility of the surface of the glans and the prepuce greatly increased. Erection takes place in the female, although to a much less extent. It engages the clitoris, bulb of the vagina, and, according to Rouget, the internal genital organs.

The exact mechanism of erection is not clearly understood. There is no doubt that the essential change is an enormous increase of the quantity of blood circulating in the part. This appears to be due (*a*) to dilation of the calibre of the arteries, and (*b*) diminution of that of the veins. The former appears to be due to inhibition of the vaso-constrictor influence, which

nominally presides over the tone of the blood-vessels, and is, accordingly, analogous to what takes place in blushing (Kolliker, &c.). Some, however, would make it to be due to the active influence of vaso-dilator nerves. The venous constriction is due to pressure of the muscles in contact with them (the deep veins by the transversus perinæi, the dorsal vein by Houston's muscles, &c.). The prevention of dilation by the passage of the veins through dense fasciæ must also be an important factor. The contraction of the smooth muscle fibres throughout the erectile tissue is probably of great importance, by preventing the return of blood from the trabecular spaces. Mere dilation of the blood-vessels, although sufficient to cause the increase of size of the organ, would never give the characters of a true erection; the rigidity must be due to muscular contraction.

The nervous centre of erection is placed in the lumbar enlargement of the cord. The *nervi erigentes* travel with the sacral nerves and the hypogastric plexus (Eckhard, Lovén). The erector nerve is stimulated by muscarin and by asphyxia; it is paralysed by atropin.

The introduction of the penis into the vagina in a state of erection determines, by reflex action, a series of rhythmic movements of the pelvis, which result in a mechanical friction of the glans and body of the penis against the labia and rugous walls of the vagina. This friction, while it increases the intensity of the erection, exalts, by degrees, the sensibility of the parts. When the voluptuous sensations have attained a certain degree of intensity, ejaculation takes place.

In the virgin female, the introduction of the penis into the vagina causes laceration of the hymen, and, in consequence, an escape of blood from the parts usually results.

During ejaculation, the perinæal muscles, especially the accelerator urinæ, undergo a series of rhythmic contractions by which the semen, which is pressed into the urethra by the contractions of the walls of the vesiculæ seminales and ductus ejaculatorii, is forcibly expelled from this tube into the fundus of the vagina, and, perhaps, into the cervix uteri. At the moment of ejaculation the voluptuous sensation, which then attains its highest limits (sexual orgasm) is accompanied by a general state of spasm, and an exaltation, physical and

psychical, of the whole organism. In the female the orgasm is accompanied by descent of the uterus, the volume of which is increased, the walls separate, and the os opens to receive the fertilizing fluid. The fimbriated extremity of the Fallopian tube is at the same time closely applied to the surface of the ovary. A very rapid increase of the secretion of the gland of Bartholin and other genital glands, amounts, at least in some cases, to an ejaculation which may or may not be simultaneous with that of the male.

When ejaculation has taken place erection ceases, and a sensation of general depression follows the previous excitement of coition.

DEATH.

In order to the existence of a living organism, the following conditions must co-exist: (1) presence of oxygen; (2) supply of nutritive material; (3) a definite organisation. The removal of any one of these is immediately followed by cessation of life.

A so-called *natural death* is excessively rare; indeed it is doubted by some whether it ever really occurs. Death is generally, if not always, due to some intercurrent disease, and is preceded by an *agony*, of which the duration and characters vary, according to the nature of the affection which brings existence to a close. The death of the body as a whole (*somatic death*) is followed by a short period during which the organs still continue to live. They soon, however, yield to the influences of the surrounding media, and *local* or *molecular death* is followed by complete disorganisation of the structures of the organism.

Somatic death is the immediate result of failure of the functions of one of the three great organs—heart, lungs, or brain (Bichat's *tripod of life*), which more obviously preside over the manifestation of the vital phenomena. Death, beginning at the heart is called *syncope*, at the lungs, *asphyxia*, at the brain, *coma*. When the action of the heart becomes gradually weaker, till at last it fails altogether, as often occurs in wasting diseases, death is said to occur by *asthenia*.

We do not purpose to enter into a consideration of the phenomena which follow the cessation of life. One of the

most interesting and important, that of cadaveric rigidity, has been already described at length.

Our task ends with the closing scene of the vital phenomena of human existence, beyond which the scope of physiological science does not extend. An inquiry into the future state of man is beyond the domain of scientific investigation, and one on which each individual must satisfy himself under the guidance of other teachers.

APPENDIX.

The following Metrical Table will be useful for convenience of reference :—

Length.		Weight.	
Millimetre,	= 0.03937 inches.	Milligramme,	= 0.015432 grains.
Centimetre	" 0.39371 "	Centigramme,	" 0.154323 "
Decimetre	" 3.93708 "	Decigramme,	" 1.543235 "
Metre,	" 39.37079 "	Gramme,	" 15.43249 "

Capacity.	
Millilitre	.. 0.061027 cubic inches.
Centilitre	.. 0.610271 "
Decilitre	.. 6.102705 "
Litre	.. 61.027052 "

The following reactions have been omitted from the body of the work :—

Of biliary acids :—

Reaction of Pderkofer.—Add to the liquid a few drops of a solution of cane-sugar (1 : 4) and some drops of concentrated sulphuric acid, keeping the temperature at about 70° C. ; a cherry red hue appears, changing to a purple. The presence of nitrates or chlorides prevents the success of this reaction. It must also be remembered that numerous other substances give a very similar reaction : albuminoids, oleic acid, phenol, benzine, salicylic acid, morphia, amylic alcohol, camphor, &c.

Reaction of Bogomoloff.—Evaporate the solution to dryness : to a little of the powdered residue, add two or three drops of concentrated sulphuric acid, then one drop of alcohol, and a series of colored zones are produced : yellow, orange, red, violet, indigo (from centre to periphery).

Reaction of Strassburg.—Dissolve some cane-sugar in the fluid ; dip in a piece of bibulous paper ; dry the latter ; then let fall a drop of concentrated sulphuric acid, and at the end of a quarter of a minute a beautiful violet coloration is seen by transmitted light.

Of bile pigments :—

Reaction of Gmelin.—Concentrated nitric acid dropped cautiously on the surface gives a series of colored rings (green, blue, violet, red and yellow) from oxidation of the pigment.

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